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Nitrogen transactions along the gastrointestinal tract of cattle: A meta-analytical approach^{1,2}

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ABSTRACT: In ruminant animals, endogenous N (EN) secretions contribute to meeting the N requirement of the ruminal microflora. The EN also constitutes a sizable portion of the duodenal N flow, which might be available to the host animal. Most measures of EN have been accomplished with highly invasive techniques or unusual semisynthetic diets. By utilizing a statistical approach and data obtained from studies reporting duodenal, ileal, and fecal N flows in cattle, the EN losses and true digestibility of N were estimated for different segments of the gastrointestinal tract of cattle. A simulation for a reference diet (24.2 g of N/kg of OM, 32% NDF and carbohydrates of medium fermentation rate) consumed at 2% of BW daily estimated that the minimal contribution of EN to the N available in

the rumen was 39%. The free EN represented 13% of the duodenal N flow, and when bacterial N of EN origin was considered, EN contributed 35% of the total N flow. The minimal entry of EN into various segments of the gastrointestinal tract was also estimated as: foregut, 10.54; small intestine, 3.10; and hindgut, 5.0 g/kg of OMI. Rumen dietary N degradability was 0.68, and true N digestibilities in the small intestine and hindgut were 0.75 and 0.49, respectively. A better understanding of the factors involved in EN losses will allow for a more accurate estimation of both N supply and N requirements. This will translate into improved accuracy of diet formulation and less N excreted into the environment.

Key words: cattle, endogenous, meta-analysis, nitrogen, requirement

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INTRODUCTION

Endogenous N (EN) secretions occur along the whole gastrointestinal (GI) tract of animals (Fuller and Reeds, 1998). The EN enters the tract either as urea or protein in secretions, or as sloughed cells (Van Bruchem et al., 1989). In ruminants, EN entering the foregut supplies ammonia and peptides to the microflora, which then provides AA to the host animal. Although the contribution of N from this source is variable, it can account for up to 60% of the ruminally available N (Siddons et al., 1985). Whereas most of the effort to date to describe N supply to ruminants has focused on characterizing the different dietary fractions (Sniffen et al., 1992), EN has received little attention (Lapierre et al., 2006), despite

its obvious significance for the ruminal microbial population.

Current estimates of EN in ruminants have been obtained using rather invasive approaches such as N-free intragastric nutrition (Orskov et al., 1986) and digesta exchange (Sandek et al., 2001), methods which may disturb normal digestive function in the experimental animals or by labeling of the animal with stable isotopes (Ouellet et al., 2002). Because these methods are labor intensive and expensive, they have provided limited amounts of data on a small number of diets.

An alternative approach to estimate EN is by statistical regression of the N apparently digested, which has been used successfully to determine true small intestinal digestibility in pigs (Fan et al., 1995) and whole tract digestibility and metabolic fecal N in ruminants (Holter and Reid, 1959).

The objective of the present study was to analyze published studies to estimate EN secretions and true N digestibility in different segments of the GI tract using statistical techniques. A better understanding of the different factors involved in EN losses will allow for a more accurate estimation of both N supply and N

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Table 1. Studies included in the database that was compiled¹

Aldrich et al., 1993	Gunter et al., 1990 ²	Remond et al., 2004 ²³⁴
Aldrich et al., 1995 ³⁴	Hannah et al., 1991 ²	Robinson et al., 1994 ²
Arieli et al., 2001 ³⁴	Hermesmeier et al., 2002	Sadik et al., 1990
Barajas and Zinn, 1998	Herrera-Saldana et al., 1990	Sairanen et al., 2005
Beauchemin et al., 2001	Ipharraguerre et al., 2002 ²	Scholljegerdes et al., 2004a ²
Beauchemin et al., 2003 ²	Ipharraguerre et al., 2005 ²	Scholljegerdes et al., 2004b ²
Bengochea et al., 2005 ³	Ipharraguerre and Clark, 2005 ²	Scholljegerdes et al., 2005 ²
Bernard et al., 2004	Joy et al., 1997 ²	Sindt et al., 2006 ³⁴
Berzaghi et al., 1996	Keery et al., 1993 ³⁴	Soto-Navarro et al., 2004
Bohnert et al., 1998 ²³⁴	Khorasani et al., 1990	Streeter et al., 1990a ³⁴
Bohnert et al., 2002	Khorasani et al., 1996 ²	Streeter et al., 1990b ²³⁴
Boss and Bowman, 1996 ²	Khorasani et al., 2001 ²	Sultan et al., 1992 ²
Bourquin et al., 1994 ³⁴	King et al., 1990 ²	Swingle et al., 1999 ³⁴
Callison et al., 2001 ²³⁴	Klusmeyer et al., 1990 ²	Taylor and Allen, 2005 ²
Cameron et al., 1991 ²	Knowlton et al., 1998	Teller et al., 1992 ²
Caton et al., 1991 ²³⁴	Koenig et al., 2003	Theurer et al., 1999 ⁴
Cecava et al., 1990 ³⁴	Krysl et al., 1991 ²	Tice et al., 1993
Cecava et al., 1991 ³⁴	Lardy et al., 1993	Valkeners et al., 2004 ²
Cecava and Parker, 1993 ³⁴	Leupp et al., 2005 ³⁴	Van Vuuren et al., 1992
Choat et al., 2002	Ludden and Cecava, 1995 ³⁴	Van Vuuren et al., 1993
Christiansen and Webb, 1990	Mabjeesh et al., 1996 ³⁴	Voelker and Allen, 2003 ²
Chung et al., 2006	May et al., 1991 ²³⁴	Yang et al., 1997 ²
Coomer et al., 1993 ³⁴	Milton et al., 1997a ²	Yang and Beauchemin, 2004 ²
Corona et al., 2006	Milton et al., 1997b	Zinn, 1990
Crocker et al., 1998 ²	Moorby et al., 2006	Zinn, 1993a
Cunningham et al., 1994 ²	Murphy et al., 1994 ²	Zinn, 1993b ²
Currier et al., 2004	Oba and Allen, 2003 ²	Zinn, 1993c ²
Doreau et al., 1993 ²	Oliveira et al., 1995 ²	Zinn, 1993d ²
Elizalde et al., 1998	Olson et al., 1994 ²	Zinn and Borques, 1993 ²
Elizalde et al., 1999 ³⁴	Ouellet et al., 2002	Zinn and Owens, 1993 ²³⁴
Erasmus et al., 1992	Overton et al., 1995 ²	Zinn and Plascencia, 1993 ²
Galloway et al., 1993 ²	Palmquist et al., 1993 ³⁴	Zinn, 1994
Garcia et al., 2000 ²³⁴	Philippeau et al., 1999 ²	Zinn and Barajas, 1997
Greenfield et al., 2001	Poore et al., 1993 ²	Zinn and Barrajas, 1997
Grigsby et al., 1992	Qiu et al., 2004	Zinn et al., 1998
Grigsby et al., 1993	Reed et al., 2006	Zinn et al., 2003

¹The search was performed in the *Journal of Animal Science* and *Journal of Dairy Science* between January 1990 and December 2006.

²Studies that included both duodenal ammonia and total duodenal N.

³Studies included in the model for prediction of N apparently digested in the small intestine.

⁴Studies included in the model for prediction of N apparently digested in the large intestine.

requirements, which will translate into more accurate diet formulation and less N excreted into the environment.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were assembled into a database from previously published studies, as described in the next section (Database Development).

Database Development

The search for studies was circumscribed to the *Journal of Animal Science* and *Journal of Dairy Science* between January 1990 and December 2006. The criteria for study inclusion into the database (Table 1) were 1) studies utilizing duodenally (or omasally) cannulated cattle (with or without ileal cannulas), with a functional rumen, which reported dietary and bacterial N, dietary

NDF and OM flows in and out of the rumen and small and large intestinal segments of the GI tract, and 2) those in which fecal N was determined. No a priori rejection criteria were set. However, a treatment within a study (Scholljegerdes et al., 2005) was excluded from the analysis because of its high N content (75.5 g of N/kg of OM).

The database comprised 29 studies with duodenally/ileally cannulated cattle and 79 studies with duodenally cannulated (or omasally sampled) cattle, 455 treatment diets, and 2,249 animal-treatment observations. Diets ranged between 3.9 and 52.1 g of N/kg of OM and between 10 and 80% NDF (Table 2). The 65 studies conducted with growing-finishing cattle included 291 treatment diets and 1,479 animal-treatment observations. Body weight of the growing-finishing cattle ranged between 68 and 690 kg. The 43 studies with lactating dairy cows included 164 treatments and 770 animal-treatment observations. The dairy cows had BW between 450 and 717 kg and were between 21 and 221 d in milk.

Table 2. Characteristics of the database compiled

Cattle type	Studies, n	Treatment diet, n		Animal characteristics			Diet characteristics			
				Days in milk, d	Milk, kg/d	Animal weight, kg	N, g/kg of OM	NDF, % OM	Grain, % diet	Intake level, % of BW daily
Lactating cows	43	164	Mean (SD)	116 (51)	26 (7)	597 (48)	29.9 (4.2)	36 (9.2)	38 (15.8)	3.0 (0.5)
			Median	108	25	610	29.7	35	41	2.9
			Minimum	21	13	450	19.6	13	0	1.4
			Maximum	221	42	717	52.1	80	75	4.4
Growing/finishing	65	291	Mean (SD)			359 (121)	22.1 (6.3)	39 (21.6)	45 (32.2)	1.9 (0.4)
			Median			345	21.5	33	50	1.9
			Minimum			68	3.9	10	0	0.5
			Maximum			690	45.7 ¹	85	90	3.7

¹A treatment within a study (Scholljegerdes et al., 2005) was omitted from the database due to its high N content (75.5 g of N/kg of OM).

Database Analysis

A multilevel model using the MIXED procedure (SAS Inst. Inc., Cary, NC) was utilized to analyze the data. Because observations within studies have more in common than observations across studies, study was analyzed as a blocking effect (St-Pierre, 2001). Furthermore, because the inferences made are for future studies, study was considered as a random effect.

The dependent variable, apparently digested N in a particular GI tract segment, was recalculated and expressed as grams per kilogram of OM entering that segment. The continuous independent variables (X_k) in the database were recalculated for the dietary k components and expressed as follows:

N entering a GI segment, as g/kg of OM;
NDF entering a GI segment, as % of OM;
concentrate, as % of OM intake (**OMI**); and
level of intake or digesta flow, as OM entering the GI segment per 100 kg of BW daily.

The rate of dietary carbohydrate degradation was also included as a categorical independent variable (C) with 3 levels, depending on grain type and grain processing: slow (whole or cracked corn, whole or cracked sorghum), medium (ground corn, ground sorghum), or fast (flaked corn, wheat, barley). A fourth category (without grain supplementation) was also considered. The results, shown in Table 3, are in comparison to the slow rate of fermentation.

To identify the most parsimonious model of N trans-actions at each segment of the GI tract, the data was fitted to the following general mixed model (St-Pierre, 2001), utilizing the corrected Akaike's information criterion for model selection (Burnham and Anderson, 1998):

$$Y_{is} = \mu + \sum (\beta_k \times X_{k(is)}) + C_{is} + M_s + \sum (B_{ks} \times X_{k(is)}) + e_{is}, \quad [1]$$

where Y_{is} = the expected outcome of the dependent variable Y (apparently digested N, g/kg of OM, in a given

GI tract segment) observed in treatment i of the study s; μ = the overall intercept across studies (fixed effect); β_k = the overall regression coefficient for variable X_k (fixed effect); $X_{k(is)}$ = the value of continuous variable X_k in study s, treatment i; C_{is} = the value of categorical variable C (carbohydrate degradation rate) in study s, treatment i; M_s = the random effect of study s; B_{ks} = the random effect of study s on the regression coefficient of Y over X_k ; and e_{is} = the unexplained residual error.

The corrected Akaike's information criterion (**CAIC**), defined as

$$CAIC = -2\ln(L) + 2k[n/(n - k - 1)], \quad [2]$$

was used for model selection, where $\ln(L)$ is the log likelihood, k is the number of parameters in the model, and n is the sample size.

The first term of CAIC is based on Kullback-Liebnier information theory, which is related to the information lost when a model is used to approximate the underlying true model. The second term takes into account the number of parameters included in the model as well as the number of observations. The CAIC provides a ranking for the models tested; the one with the lowest CAIC value can then be selected for inference because it is the model estimated to be closer to the unknown function that generated the data (Burnham and Anderson, 1998). The CAIC, however, might include fixed effects that, although they improve the overall fit of the model, are not significant at $P < 0.05$.

The CAIC offers many advantages over the more classical model selection by hypothesis testing approach. Stepwise procedures often yield different results if a forward or backward algorithm is performed. Testing schemes are based on subjective α -levels, sometimes as high as 0.15. However, a large α -level leads to overfitted models (Burnham and Anderson, 1998), resulting in a reduction of the overall model bias but an increase in the variance of the parameters and wider confidence intervals for the estimated parameters. Although non-nested models cannot be evaluated by hypothesis testing, information criteria allow for the evaluation of any type of model, provided they are based on the same data.

Table 3. Regression coefficients for the fixed effects of the mixed models that best fitted the dependent variables

Item ¹	Intercept	N, g of N/kg of OM	NDF, % of OM	Concentrate, % of OM	Carbohydrate fermentation rate ²			Intake level, ³ % of BW daily	n ⁴
					Fast	Medium	None		
TTD N, g of N/kg of OMI	-3.32 (0.47) ⁵	0.84 (0.02)	-0.04 (0.01)		0.75 (0.18)	0.20 ⁶ (0.23)	0.68 (0.31)		454
RAD N, g of N/kg of OMI	-13.63 (1.09)	0.51 (0.04)			-1.23 (0.38)	-0.82 ⁶ (0.47)	-0.43 ⁶ (0.53)	0.54 ⁶ (0.37)	454
RTD N, g of N/kg of OMI	-4.90 (1.36)	0.68 (0.04)	-0.03 ⁶ (0.02)		0.44 ⁶ (0.39)	0.64 ⁶ (0.49)	0.32 ⁶ (0.68)	0.95 (0.41)	425
BactN, g of N/kg of OMI	9.29 (0.76)	0.14 (0.03)			1.63 (0.30)	1.26 (0.37)	-0.20 ⁶ (0.44)		425
SID N, g of N/kg of duodenal OM	-12.43 (2.16)	0.75 (0.04)		0.05 (0.01)				4.18 (1.05)	117
LID N, g of N/kg of ileal OM	-21.54 (4.2)	0.49 (0.09)			1.09 ⁶ (1.03)	-0.15 ⁶ (1.11)	0.92 ⁶ (1.83)	11.7 (3.33)	120
RAD OM, g of OM/kg of OMI	517.9 (34)	-0.67 ⁶ (0.88)	-1.43 (0.44)		35.5 (9.5)	14.3 ⁶ (11.7)	39.4 (16.8)	-12.0 ⁶ (10.1)	422
SID OM, g of OM/kg duodenal OM	316 (111)	3.67 (1.39)	-7.20 (0.93)		22.2 ⁶ (22)	27.2 ⁶ (19)	NA ⁷	166.2 ⁶ (59)	45

¹TTD N = total tract apparently digested N; OMI = OM intake; RAD N = ruminal apparently digested N; RTD N = ruminal truly digested N; BactN = Bacterial N flow at the duodenum or omasum; SID N = small intestinal apparently digested N; LID N = large intestinal apparently digested N; RAD OM = ruminal apparently digested OM; and SID OM = small intestinal apparently digested OM.

²Values are expressed in relationship to the slow carbohydrate fermentation rate.

³Digesta entering the segment.

⁴Number of treatment diets.

⁵Values in parentheses are SE.

⁶Not different from zero, $P > 0.05$. All other coefficients were significantly different from zero at a $P < 0.05$.

⁷NA = not available; no diet without grain supplementation was part of the database.

Because least squares means of the variables are not estimated with equal accuracy across different studies, weighting the means using the inverse of the SE is highly desirable (St-Pierre, 2001). In this analysis, however, data were recalculated and thus the SE of the generated variables could not be estimated. The inverse of the square root of n (number of observations in the reported mean) was used instead (i.e., it was assumed that all the studies shared the same variance for a given variable).

Observed values of the dependent variables (Y_{is}) come from a multidimensional space, and because it is of interest to represent the data solely as function of the main variable of interest (N entering a particular segment of the GI tract), the value of the observations was adjusted for the lost dimensions (St-Pierre, 2001). However, this adjustment has to be done to a diet of reference (described below) instead of forcing additional variables to zero. The adjusted values for the dependent variables (\hat{Y}_{is}) were also adjusted for study effect (random effect) by rearranging the terms in Eq. [1] as follows:

$$Y_{is} - \sum (\beta_k \times (X_{k(is)} - RD_k)) - (C_{is} - MF) - M_s - \sum [B_{ks} \times (X_{k(is)} - RD_k)] = \mu + \beta_N \times X_{N(is)} + e_{is}, \quad [3]$$

and

$$\hat{Y}_{is} = \mu + \beta_N \times X_{N(is)} + e_{is}, \quad [3']$$

where \hat{Y}_{is} = adjusted value of the dependent variable for the i treatment in the s study; and RD_k = value of the k component of the reference diet or digesta. The reference diet composition, on an OM basis, was 32% NDF, 40% concentrate of medium rate of fermentation, and ingested at a rate of 2% of BW daily (level of digesta flow at the duodenum and ileum was calculated utilizing similar meta-analytical techniques and for this diet was 1.1 and 0.64% of BW daily, respectively); MF = the adjustment of the carbohydrate fermentation rate to a medium rate; β_N = the regression coefficient for variable X_N ; and X_N = the value of the continuous variable N entering the GI segment in study s, treatment i, and the rest of the variables are as defined for Eq. [1].

Residuals of the mixed model were analyzed for normality (normal distribution plot) and homoscedasticity (residual plot; shown in Figures 1, 6, 8, and 10).

The predictions of the fixed model were regressed against the complete mixed model to evaluate the predictive value of the fixed effects of the model. A high coefficient of determination (r^2) indicates a small contribution of the random component (study).

The OM disappearance in the rumen and small intestine was analyzed utilizing the methods described above (Table 3). The flow of OM in the digesta was estimated and used to calculate the N content of the digesta per kilogram of OM, which was then employed

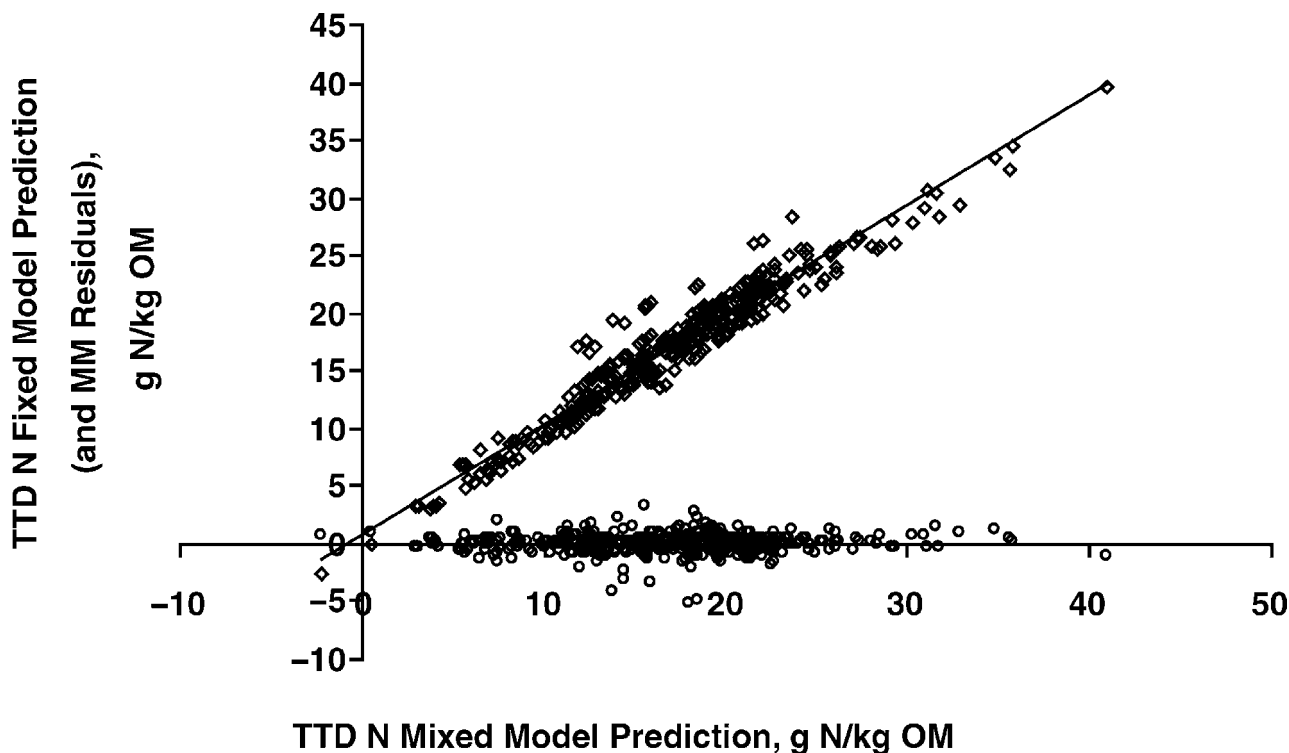


Figure 1. Prediction (\diamond) of the fixed components of the mixed model vs. the mixed model prediction for total tract digested N (TTD N). Residuals (\circ) of the mixed model are also shown in the graph. The linear regression was fixed model = $(0.96 \times \text{mixed model}) + 0.72$ ($r^2 = 0.940$).

in the integration of N transactions along the whole GI tract.

RESULTS

The total tract apparently digested N (**TTD N**) was best predicted when N, NDF content of the diet, and rate of carbohydrate fermentation were included in the model (Table 3). The residual analysis of the mixed model showed no trend, and residuals were normally distributed around zero (Figure 1). The fixed components of the model were able to explain most of the variation ($r^2 = 0.94$, Figure 1) of the mixed model, implying that the effect of the random variable (study) had a small impact on the prediction of TTD N. When the adjusted TTD N was regressed against the dietary N (Figure 2) it showed an intercept of -4.3 g of N/kg of OMI and a slope of 0.84. Thus, for the reference diet the true digestibility of N was 0.84 and the metabolic fecal N (**MFN**) was 4.3 g of N/kg of OMI.

Duodenal N has been reported as total N or as nonammonia-N (**NAN**) by different authors. Because some studies have reported both (Table 1), a direct relationship between total N and NAN could be established (Figure 3). Based on this relationship, data reported as NAN were used to calculate total N entering the duodenum.

The mixed model that best described the ruminal apparently digested N (**RAD N**) included N content of

the diet, intake level, and rate of carbohydrate fermentation (Table 3). The residual plot of the mixed model indicated residuals were normally distributed around zero and no trend was evident (not shown). The fixed model explained only 50% of the prediction made by the mixed model (Figure 4). The adjusted RAD N, as well as the raw data, plotted against the dietary N are shown in Figure 5. For the reference diet, the ruminal N apparent digestibility was 0.51 and the foregut apparent EN was 13.4 g of N/kg of OMI.

The model for the prediction of ruminal truly digested N, calculated as the difference between N intake and duodenal N flow minus microbial N, included N and NDF content of the diet, intake level, and rate of carbohydrate fermentation (Table 3). The residual plot for the mixed model showed residuals normally distributed with mean zero, and no trend was evident (Figure 6). The fixed model explained approximately 72% of the predictions made by the mixed model. When the adjusted ruminal truly digested N was regressed against the dietary N (Figure 7), it showed an intercept of -3.17 g of N/kg of OMI and a slope of 0.68. Thus, for the reference diet the true ruminal digestibility of dietary N was 0.68 and the EN reaching the duodenum was 3.17 g of N/kg of OMI.

The model for the prediction of bacterial N (**BactN**) passage to the duodenum included N and rate of carbohydrate fermentation (Table 3). The residual plot for the mixed model showed residuals normally distributed

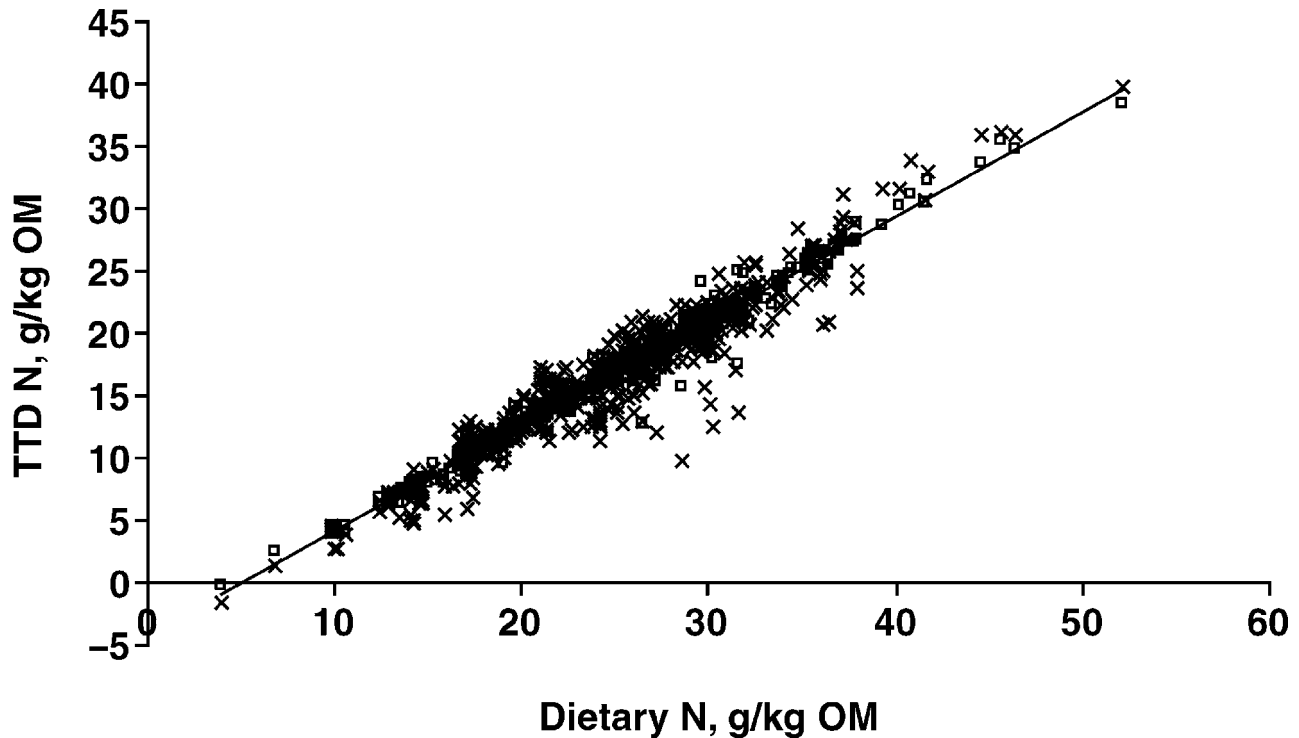


Figure 2. Total tract digested N (TTD N) as function of dietary N content. Raw (crosses) and reference diet adjusted (squares) data are shown in the graph. The regression equation for the adjusted data was $\text{TTD N} = [0.84 (\pm 0.006) \times \text{dietary N}] - 4.31 (\pm 0.148) \text{ g of N/kg of OMI}$ ($r^2 = 0.979$). Data were adjusted to a reference diet with a NDF content of 32% and carbohydrates of medium fermentation rate, ingested at an intake level of 2% of BW daily.

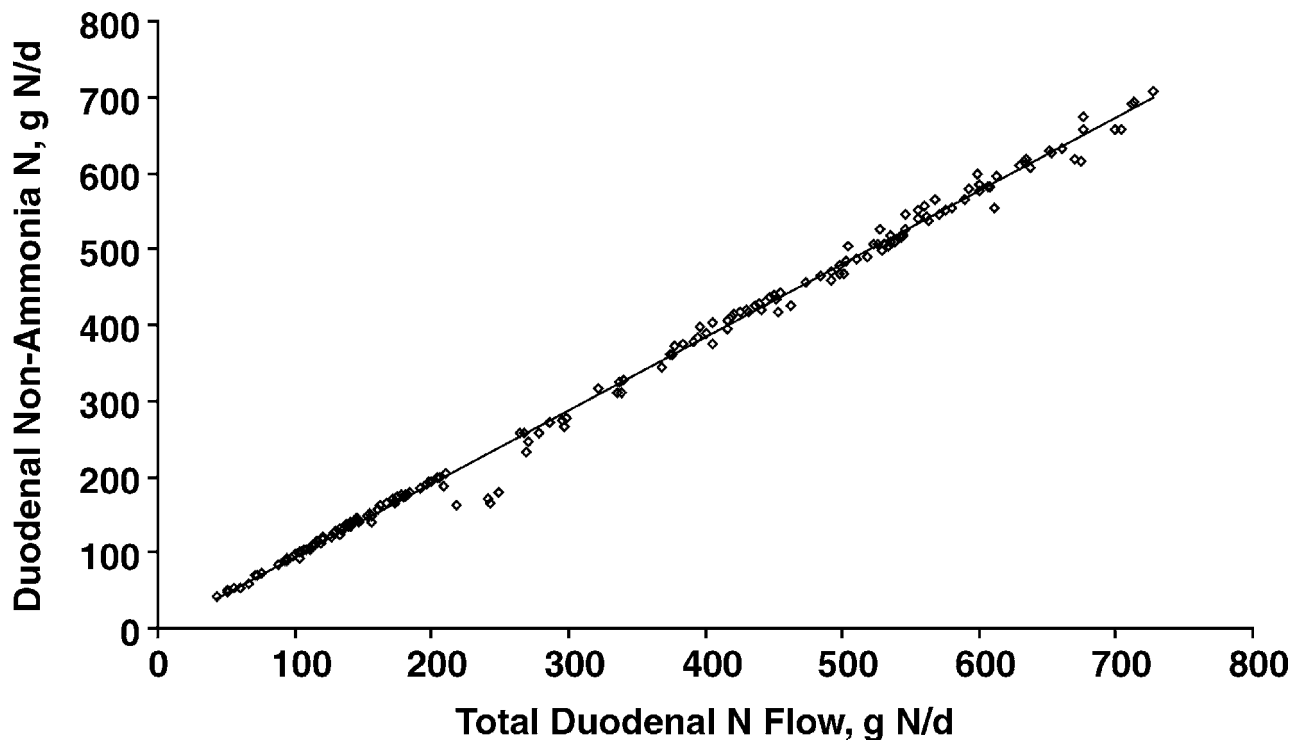


Figure 3. Relationship between total duodenal N flow and duodenal nonammonia N. Data were obtained from 47 studies reporting 194 treatment diets. The intercept of the regression was not different from zero, and the regression was forced through the origin. The resulting regression was $y = [0.959 (\pm 0.002) \times \text{total duodenal N}]$ ($r^2 = 0.999$).

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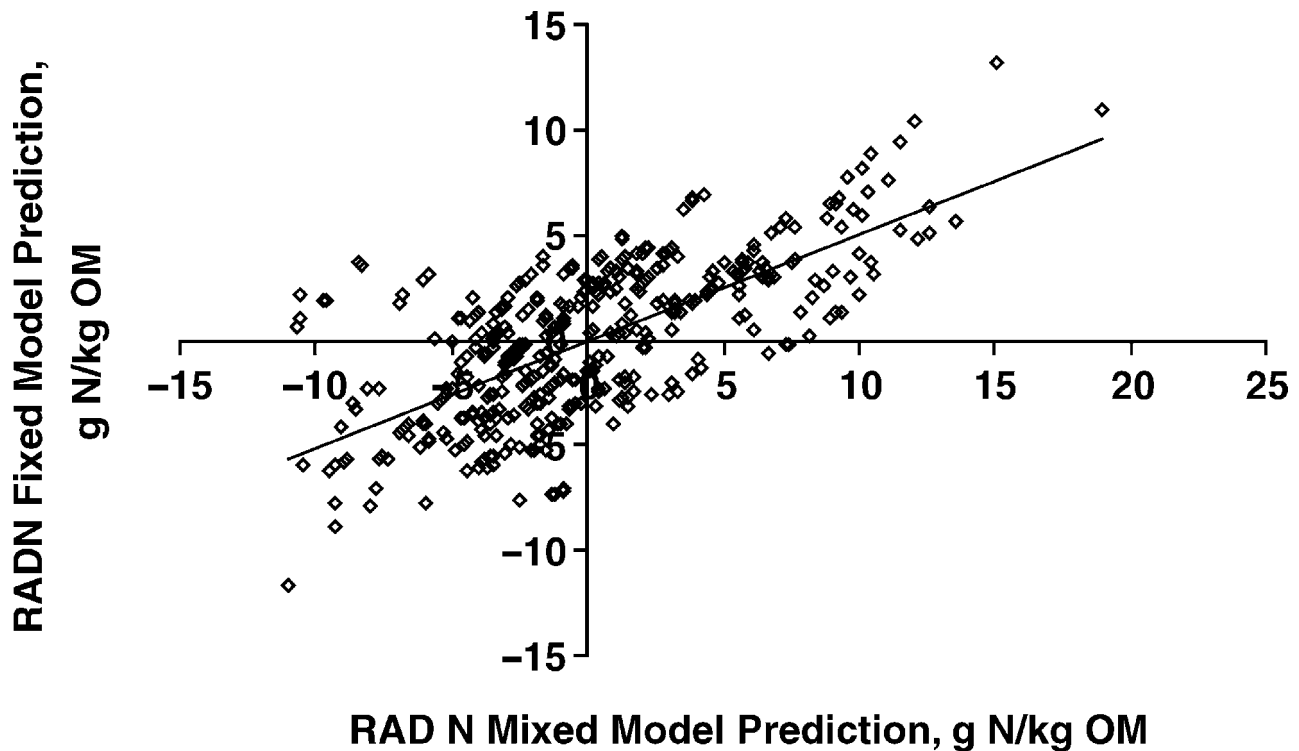


Figure 4. Prediction of the fixed components of the mixed model vs. the mixed model prediction for ruminal apparently digested N (RAD N). Residuals of the mixed model were omitted from the graph for clarity. The linear regression was fixed model = $(0.51 \times \text{mixed model}) - 0.05$ ($r^2 = 0.503$).

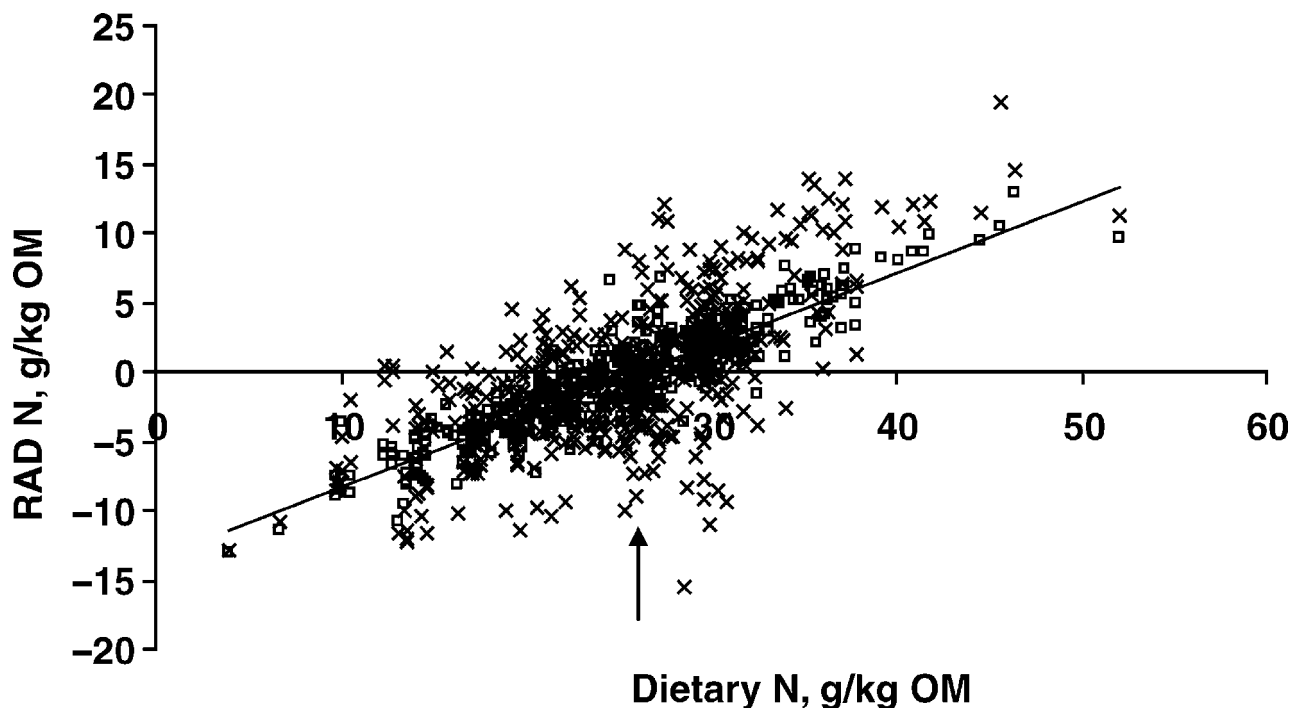


Figure 5. Ruminal N balance (ruminal apparently digested N, RAD N) as a function of dietary N content. Raw (crosses) and reference diet adjusted (squares) data are shown in the graph. The regression equation was $\text{RAD N} = [0.51 (\pm 0.011) \times \text{dietary N}] - 13.36 (\pm 0.292)$ g of N/kg of OMI ($r^2 = 0.819$). The arrow represents the dietary N content at which the ruminal N balance becomes zero. Data were adjusted to a reference diet with a NDF content of 32% and carbohydrates of medium fermentation rate, ingested at an intake level of 2% of BW daily.

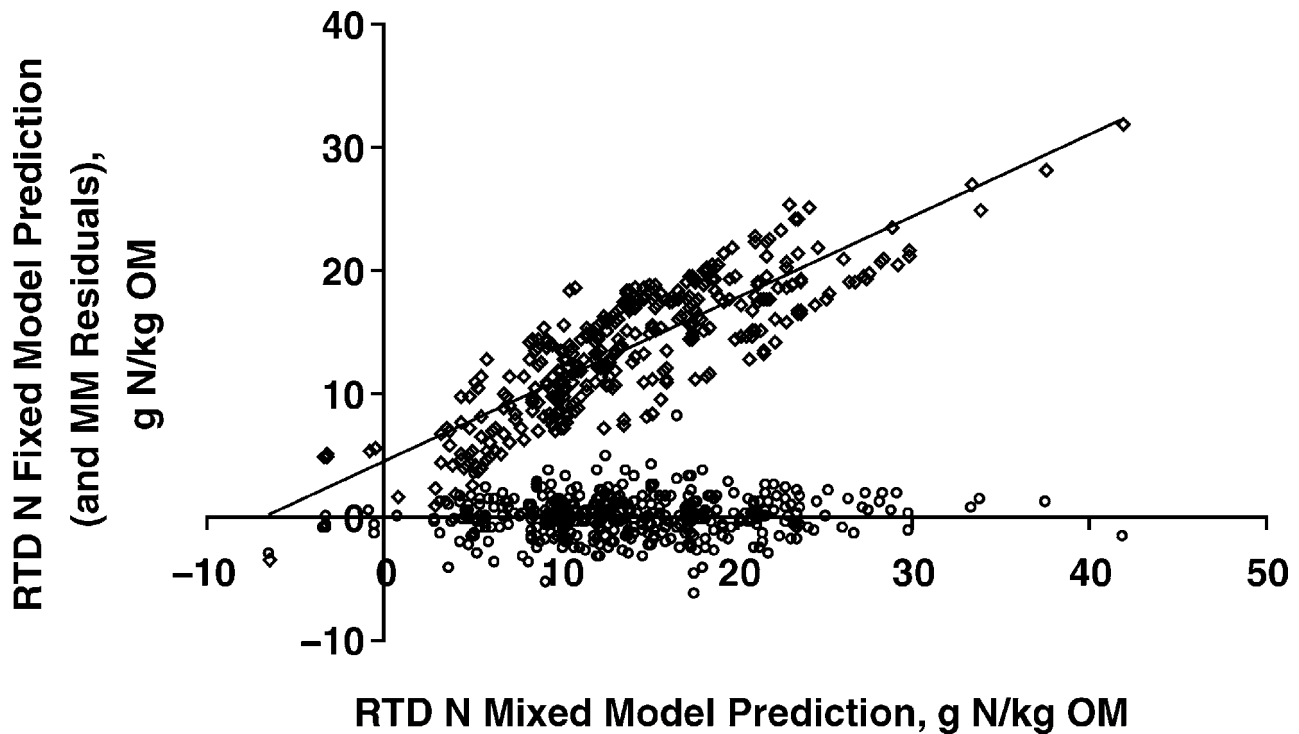


Figure 6. Prediction (\diamond) of the fixed components of the mixed model vs. the mixed model prediction for ruminal truly digested N (RTD N). Residuals (\circ) of the mixed model are shown in the graph. The linear regression was fixed model = $(0.668 \times \text{mixed model}) + 4.41$ ($r^2 = 0.716$).

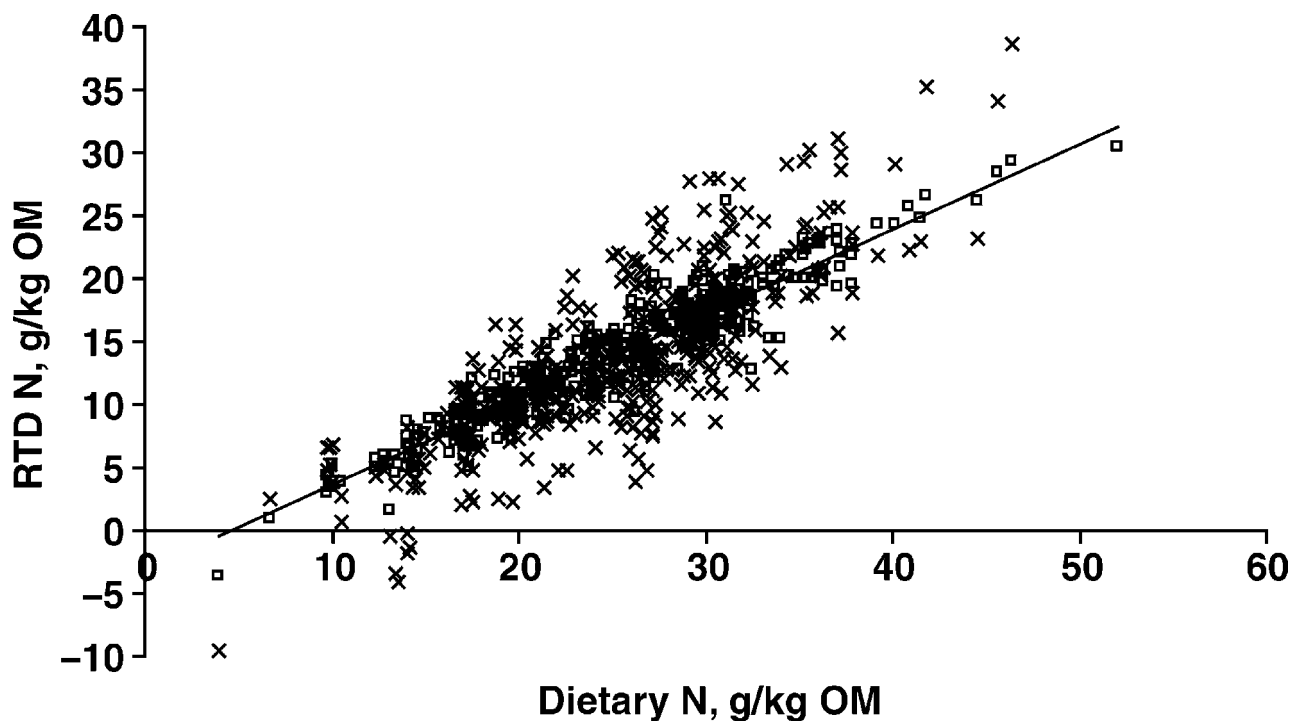


Figure 7. Ruminal truly digested N (RTD N) as a function of dietary N content. Raw (crosses) and reference diet adjusted (squares) data are shown in the graph. The regression equation was $\text{RTD N} = [0.676 (\pm 0.011) \times \text{dietary N}] - 3.17 (\pm 0.292)$ g of N/kg of OMI ($r^2 = 0.895$). Data were adjusted to a reference diet with a NDF content of 32% and carbohydrates of medium fermentation rate, ingested at an intake level of 2% of BW daily.

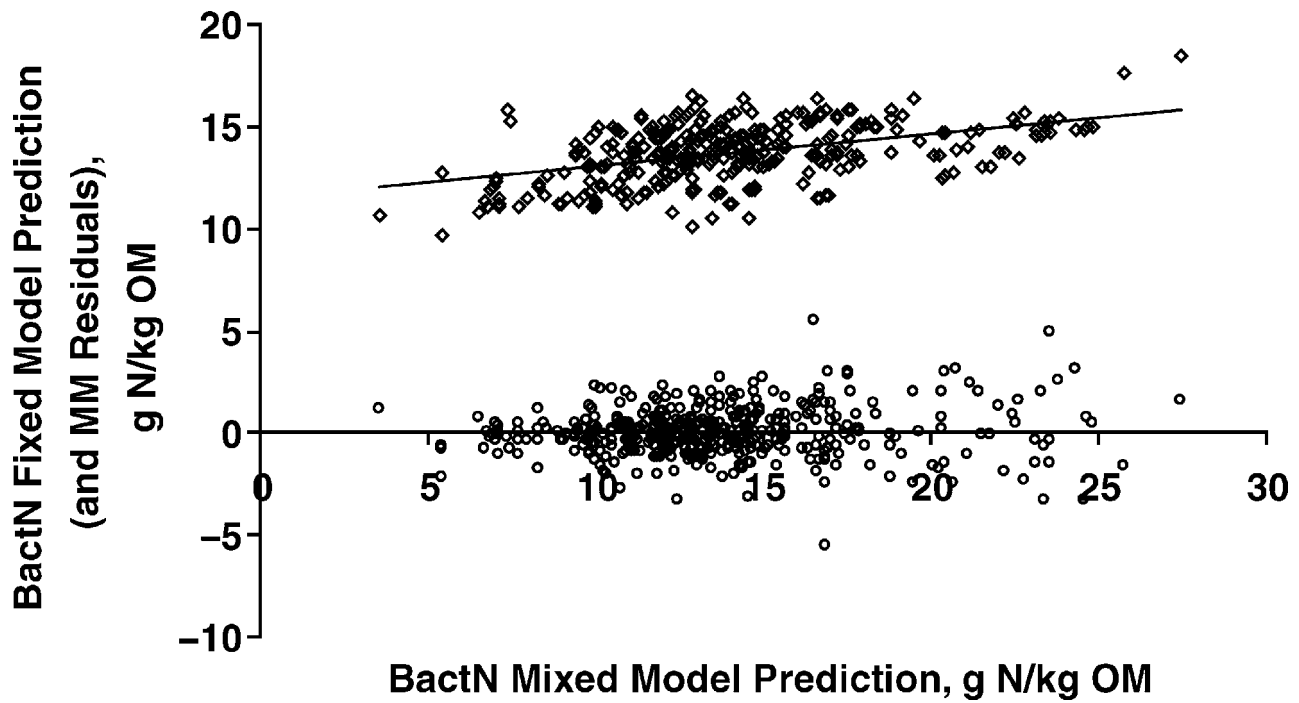


Figure 8. Prediction (\diamond) of the fixed components of the mixed model vs. the mixed model prediction for bacterial N (BactN) yield. Residuals (\circ) of the mixed model are shown in the graph. The linear regression was fixed model = $(0.16 \times \text{mixed model}) + 11.41$ ($r^2 = 0.197$).

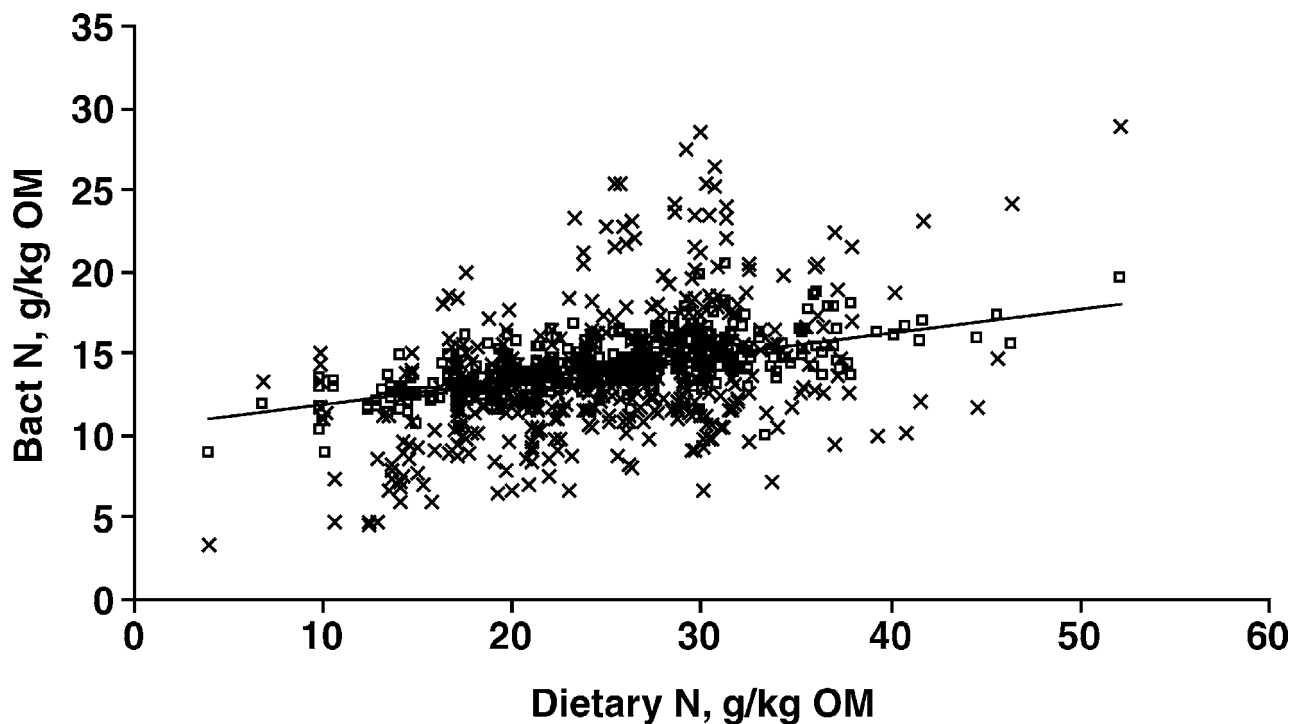


Figure 9. Bacterial N (BactN) yield as a function of dietary N content. Raw (crosses) and reference diet adjusted (squares) data are shown in the graph. The regression equation was $\text{BactN} = [0.145 (\pm 0.008) \times \text{dietary N}] + 10.54 (\pm 0.219)$ g of N/kg of OMI ($r^2 = 0.407$). Data were adjusted to a reference diet with a NDF content of 32% and carbohydrates of medium fermentation rate, ingested at an intake level of 2% of BW daily.

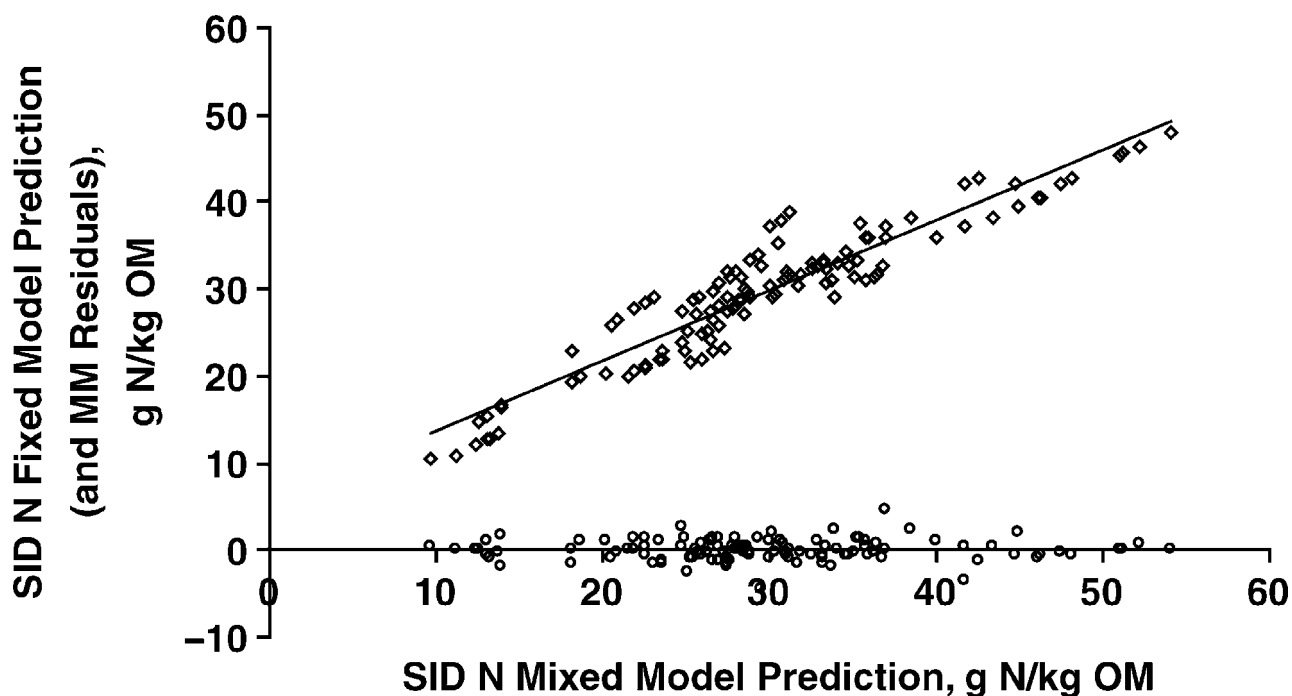


Figure 10. Prediction (\diamond) of the fixed components of the mixed model vs. the mixed model prediction for small intestine digested N (SID N). Residuals (\circ) of the mixed model are shown in the graph. The linear regression was: fixed model = $(0.812 \times \text{mixed model}) + 5.46$ ($r^2 = 0.882$).

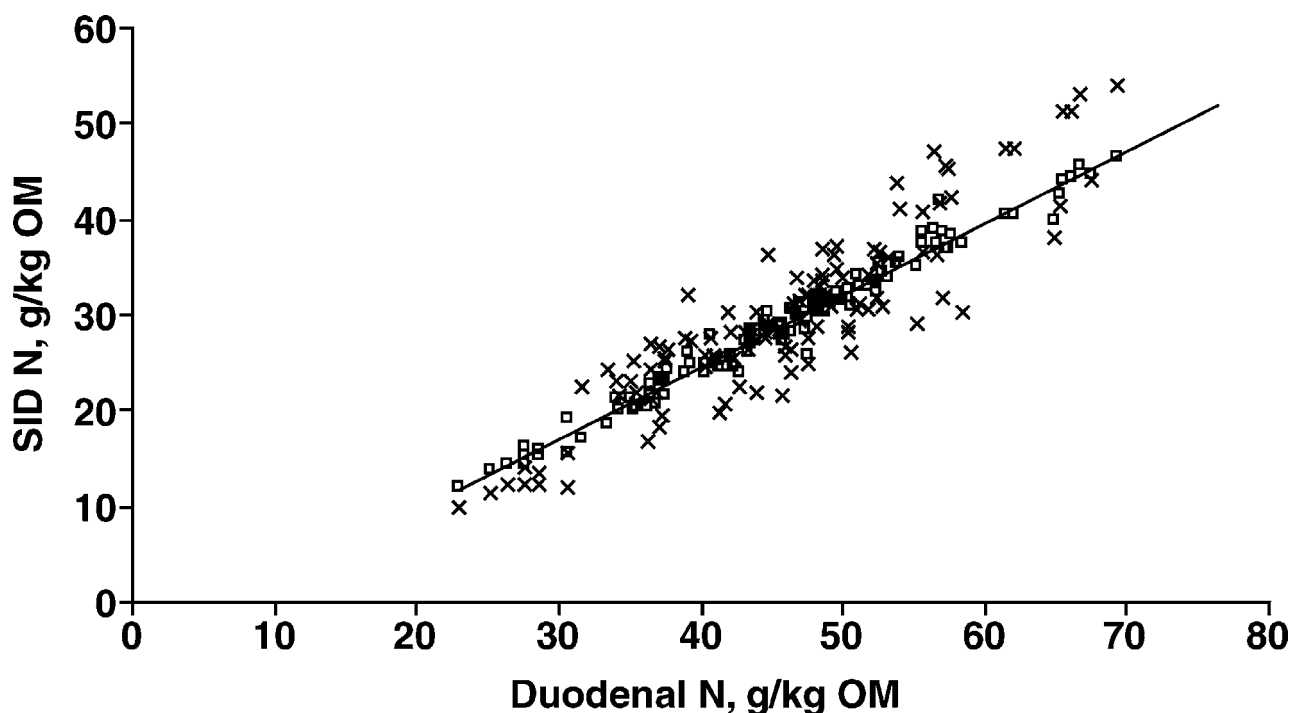


Figure 11. Small intestine digested N (SID N) as a function of duodenal N content. Raw (crosses) and reference diet adjusted (squares) data are shown in the graph. The regression equation was $\text{SID N} = [0.754 (\pm 0.01) \times \text{duodenal N}] - 5.60 (\pm 0.53)$ g of N/kg of duodenal OM ($r^2 = 0.974$). Data were adjusted to a reference diet with a NDF content of 32% and carbohydrates of medium fermentation rate, with a duodenal passage rate of 1.1% of BW daily.

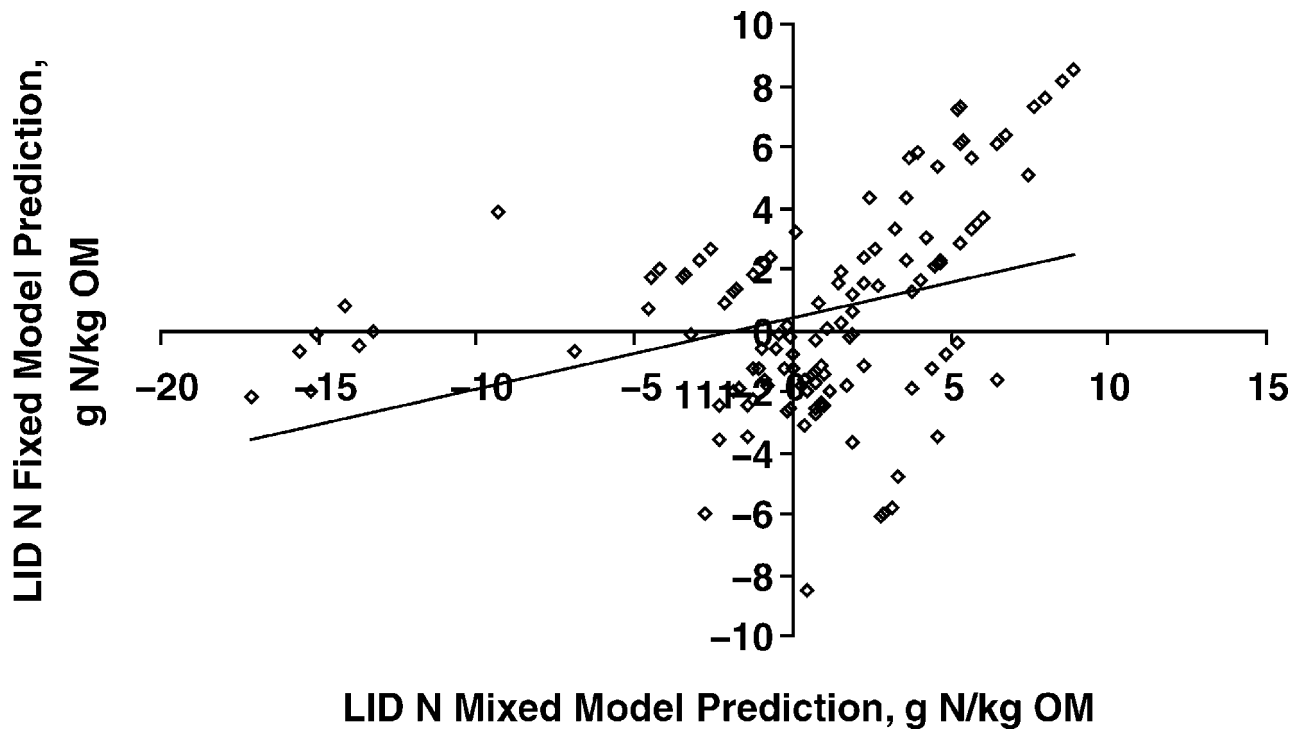


Figure 12. Prediction of the fixed components of the mixed model vs. the mixed model prediction for large intestine digested N (LID N). Residuals of the mixed model were omitted from the graph for clarity. The linear regression was fixed model = $(0.233 \times \text{mixed model}) + 0.39$ ($r^2 = 0.128$).

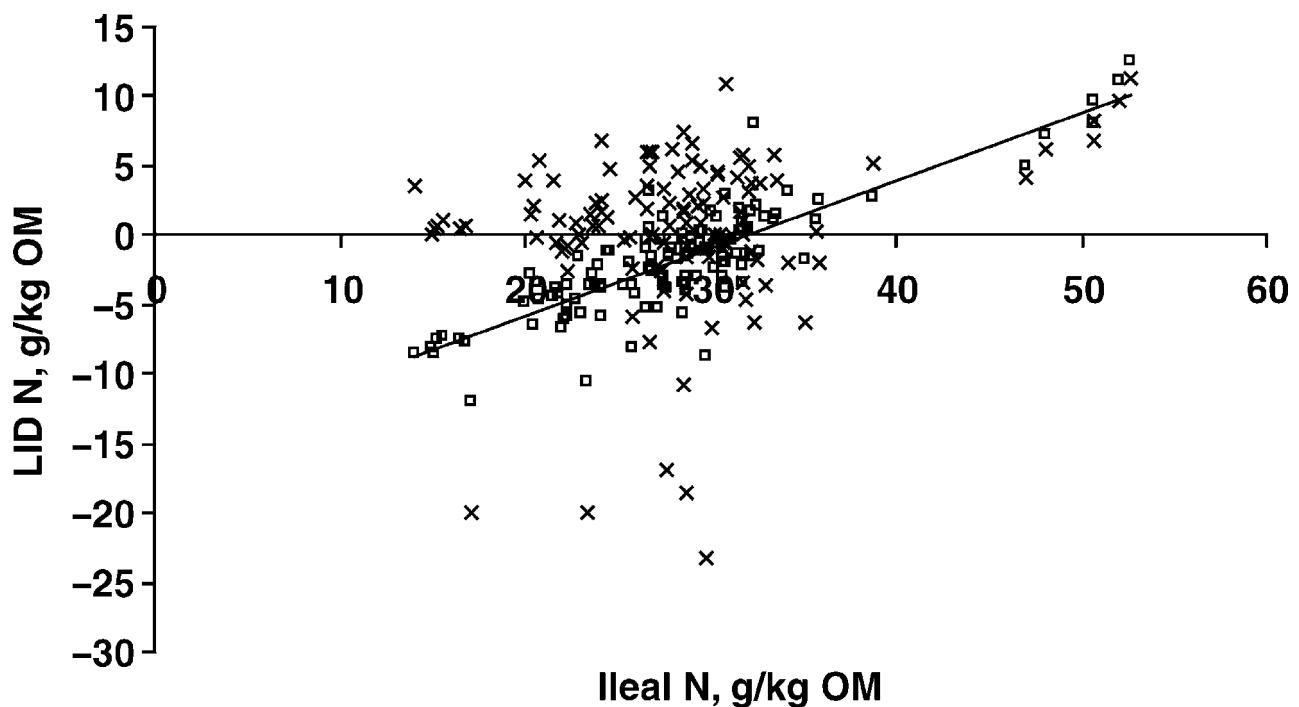


Figure 13. Large intestine digested N (LID N) as a function of ileal N content. Raw (crosses) and reference diet adjusted (squares) data are shown in the graph. The regression equation was $\text{LID N} = [0.489 (\pm 0.28) \times \text{ileal N}] - 15.62 (\pm 0.80)$ g of N/kg of ileal OM ($r^2 = 0.727$). Data were adjusted to a reference diet with a NDF content of 32% and carbohydrates of medium fermentation rate, with an ileal passage rate of 0.64% of BW daily.

with mean zero, and no trend was evident (Figure 8). The fixed model explained approximately 20% of the predictions made by the mixed model. When the adjusted BactN was regressed against the dietary N (Figure 9) it showed an intercept of 10.5 g of N/kg of OMI and a slope of 0.15.

Based on 117 treatment diets in 26 studies, the model for the prediction of small intestine apparently digested N (**SID N**) included N, concentrate content of the diet, and intake level (Table 3). The residual plot for the mixed model showed residuals normally distributed with mean zero and no evident trend (Figure 10). The fixed model explained approximately 88% ($r^2 = 0.882$) of the predictions made by the mixed model. The adjusted SID N, as well as the raw data, plotted against the duodenal N are shown in Figure 11. For the reference diet the small intestinal N digestibility was 0.75 and the EN reaching the ileum was 5.6 g of N/kg of duodenal OM.

The model that best predicted large intestine digested N (**LID N**) included N, rate of dietary carbohydrate fermentation, NDF entering the large intestine, and intake level. However, only 38 dietary treatments in 8 studies reported NDF reaching the hindgut, and because data were limited, this variable was removed from the model. The analysis was then performed on 120 dietary treatments in 26 studies and results are shown in Table 3. The residual plot showed residuals normally distributed with mean zero and no trend was evident, but residuals showed high dispersion (data not shown). The fixed model explained approximately 13% ($r^2 = 0.128$) of the predictions made by the mixed model (Figure 12). The adjusted LID N, as well as the raw data plotted against the ileal N, is shown in Figure 13. For the reference diet the large intestinal N digestibility was 0.49 and the EN appearing in the feces was 15.6 g of N/kg of ileal OM.

The mixed model that best predicted the ruminal apparent digestibility of OM included dietary N, NDF, rate of carbohydrate fermentation, and intake level (Table 3). To estimate the passage of OM into the duodenum, the reference diet with a dietary N content of 24.2 g/kg of OM was utilized and yielded a value of 0.55 kg of duodenal OM/kg of OMI. Likewise, the model that best predicted the small intestinal apparent digestibility of OM included duodenal N, duodenal NDF, rate of carbohydrate fermentation, and level of digesta passing into the duodenum (Table 3). For the reference diet, a value of 0.58 kg of ileal OM/kg of duodenal OM was estimated.

DISCUSSION

Current estimates of MFN have been determined by regression analysis or by feeding protein-free diets to the experimental animals (NRC, 2001). Swanson (1977) calculated a MFN of 4.7 g of N/kg of DMI from data for cattle fed 70 natural and semisynthetic very low protein diets. Limitations of the protein-free diet approach are

that, by design, these diets are rather unusual; that feed intake is usually reduced when N is deficient; and that animals might adapt to the low protein diets ingested and thus the estimates obtained might not represent the MFN under normal feeding conditions. An alternative is to obtain MFN estimates by regressing TTD N vs. N intake (or N content of the diet). Different values for the MFN have been obtained utilizing the regression approach (2.9 g of N/kg of DMI, Waldo and Glenn, 1984; 3.48 g of N/kg of DMI, Holter and Reid, 1959; 4.3 g of N/kg of DMI, Jonker et al., 1998; 4.8 to 5.5 g of N/kg of DMI, Kauffman and St-Pierre, 2001). These estimates, however, ignore the fact that more factors might be involved in determining EN losses. In the current study, the TTD N was affected not only by the N content of the diet, but also by NDF content and the fermentation rate of dietary carbohydrates. Although NDF reduced the apparently digested N, rapidly fermenting carbohydrates increased the total tract digestibility. Thus, slow fermenting carbohydrates might reach the lower gut where they provide energy to the resident microbes, stimulating hindgut fermentation and trapping of N, which then appears in the feces. When the multidimensionality of MFN losses were taken into account (Figure 2), an estimate of 4.3 g of N/kg of OM for the reference diet (32% NDF, carbohydrates medium fermentation rate) was obtained. This value, when expressed in DM (3.96 g of N/kg of DM, assuming an OM content of 0.92), is lower than the one reported by Swanson (1977) and used by the NRC since 1985 (NRC, 1985). Ignoring the multidimensionality of MFN losses, however, a value of 3.04 g of N/kg of DM (from 3.3 g of N/kg of OM in Table 3) is obtained, closer to the one reported by Holter and Reid (1954) in which low fiber-high protein lush forages were fed.

The slope of the regression for TTD N in the present analysis indicated that the true digestibility of the dietary N was 0.84. The high coefficient of determination ($r^2 = 0.98$) indicates that N behaves as a uniform fraction in the GI tract of ruminants, which is a requirement for this type of statistical analysis (Van Soest, 1994). Almost identical values for the total tract true digestibility of N (0.83) have been previously reported (Jonker et al., 1998; Kauffman and St-Pierre, 2001), although a wider range can be found in the literature ranging from 0.76 (Kohn et al., 2005) to 0.95, for green forages (Holter and Reid, 1959).

For TTD N, the random effects of the mixed model explained a small proportion of the mixed model (~6%). This was the smallest study effect observed for any of the variables analyzed. The estimation of TTD N is relatively direct, compared with the other variables analyzed, depending only on N intake and fecal N excretion. However, good study agreement does not necessarily imply that a true value was obtained. The N balance technique is known to systematically overestimate N retention (Macrae et al., 1993), and even in the most carefully controlled conditions (Rasch and Benevenga, 2004) not all the N could be accounted for. Methods

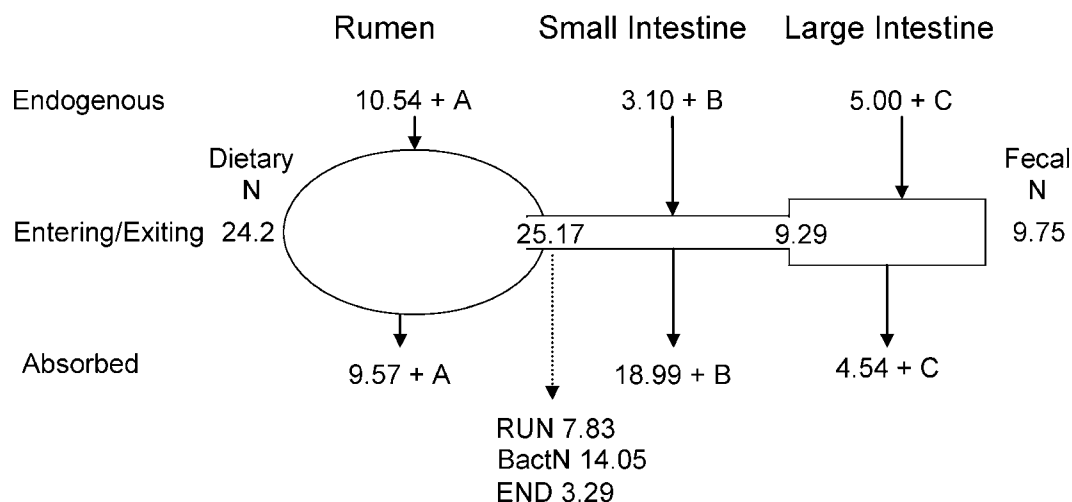


Figure 14. Nitrogen transactions along the gastrointestinal tract of cattle for an example diet (32% NDF, carbohydrates of medium degradation rate, consumed at 2% of BW daily, on an OM basis) containing 24.2 g of N/kg of OM. All fluxes expressed in g of N/kg of OM intake. Nitrogen entering the small intestine is composed of ruminal undegraded feed N (RUN), bacterial N (BactN), and free endogenous N reaching the duodenum (END). The estimates for the endogenous N entering each compartment are minimal estimates, which is indicated by the letters A, B, and C.

used for handling and drying feces (both oven and freeze-drying) has been shown to cause the loss of a substantial fraction of fecal N (Spanghero and Kowalski, 1997). It seems that oven-drying feces at 60°C can cause a loss of ~15% of the fecal N (Flatt et al., 1961; Juko et al., 1961), and higher losses can occur at higher temperatures (Hutchinson and Morris, 1936). Because feces were oven-dried or freeze-dried in the studies analyzed, values reported in the present work might include a systematic bias.

Ruminal N balance was negative when the dietary content of N was low, becoming neutral when the diet of reference reached 26.2 g of N/kg of OM (Figure 5). This implies that, when expressed on a DM basis, diets with less than 15.1% CP resulted in a net gain of N during their passage through the rumen. Ruminal N balance is an indirect indicator of N availability for microbial protein synthesis (NRC, 2001), and negative N balances maximize the usage of N. Rapidly fermenting carbohydrate further increased the utilization of ruminal N, reducing ruminal N balance. Increasing the rate of carbohydrate fermentation for the diet of reference would increase the point (29.2 g of N/kg of OM) at which ruminal N balance becomes neutral, consistent with an increased supply of energy for microbial growth and more efficient capture of ruminal N.

The true ruminal digestibility of N was 0.68 and the free EN exiting the foregut for the reference diet was 3.17 g of N/kg of OMI (Figure 7). Most studies used duodenally cannulated animals, thus this estimate includes abomasal secretions and, at least in theory, should be higher than omasal EN passage. However, actual measurements in both omasal and duodenal samples have been unable to detect any difference regarding of N passage (Punia et al., 1989; Ahvenjarvi et

al., 2000). Although NDF and carbohydrate fermentation rate were included in the model (Table 3), the estimates were not different than zero. These variables are unlikely to affect the true digestibility of dietary N or the EN entering the foregut. In a recent study utilizing ¹⁵N labeling of the experimental animals, Ouellet et al. (2002) determined that the EN exiting the foregut was not affected by fiber content of the diet and was 2.4 or 4.6 g of N/kg of OMI, depending on the precursor pool for EN synthesis considered (mucosal or plasma pools, respectively). Level of intake, however, reduced the amount of EN per kilogram OM exiting the foregut and it was likely because of the shorter residence time of the feed in this part of the GI tract or dilution by the larger feed intake (Table 3). A reduction in abomasal EN secretions per kg of OMI with increasing feed intake has been reported previously in steers (Hart and Leibholz, 1990). Estimations of EN reaching the duodenum using low protein diets (~2.1 g of N/kg of DMI, Brandt et al., 1980; 8.5 g of N/kg of DMI, Hart and Leibholz, 1990) or intragastric infusion of nutrients (58 mg of N/kg of BW^{0.75}; Orskov et al., 1986) have yielded disparate values for the duodenal flow of EN. The NRC (2001) has adopted a value of 1.9 g of N/kg of DMI based on these studies. However, this value is subject to the same criticisms made to the use of low protein diets for the estimation of MFN and might not be directly applicable to animals under common feeding practices.

The fixed effects of the mixed model were poor predictors ($r^2 = 0.197$; Figure 8) of BactN passage to the duodenum. Because microbial metabolism in the rumen is regulated primarily by the amount and fermentation rate of carbohydrates (Stern et al., 1994), microbial production was not adequately captured by the simple description of these parameters in the model employed.

However, the determination of microbial yield relies on many different factors that might contribute to the large interstudy variability observed. Most studies utilized purines as an internal microbial marker, but a few used diaminopimelic acid or ^{15}N . Purines were generally analyzed utilizing the method of Zinn and Owens (1986), but numerous authors have introduced modifications which affect the final values obtained (Obispo and Dehority, 1999). Even when different research centers agreed to follow a set protocol for the determination of diaminopimelic acid, interlaboratory variability was observed (Robinson et al., 1990). Microbial marker choice (Siddons et al., 1982; Perez et al., 1996), markers to determine digesta flow (Egan and Doyle, 1984; Faichney and White, 1988), type of cannula and cannula placement (Robinson and Kennelly, 1990; Harmon and Richards, 1997), microbial isolation and sample handling (Siddons et al., 1982; Whitelaw et al., 1984; Stern et al., 1994), and sampling protocol (Gill et al., 1999) were also likely to affect the outcome of this measurement (Ahvenjarvi et al., 2000).

Dietary N increased BactN yield with an efficiency of 0.15 (Figure 9), which might be related to a higher microbial efficiency when preformed AA are available. Assuming that 60% of the dietary OM was truly digested in the rumen, microbial efficiency ranged from 20 to 27.5 g of BactN/kg of OM fermented for diets ranging from 10 to 40 g of N/kg of OMI. This range falls well within the large range reported in the literature (12 to 54 g of BactN/kg of OM fermented; NRC 2001). The intercept of the BactN equation (10.54 g of BactN/kg of OMI) represents the amount of EN incorporated into microbial nitrogenous compounds when the animals are fed a N-free diet.

Similar to the rumen, the level of duodenal digesta flow decreased the small intestinal EN, possibly because of an increase in transit time or by dilution by the larger duodenal flow (Table 3). The true small intestinal digestibility of N and the EN reaching the ileum for the reference diet were 0.75 and 5.23 g of N/kg of duodenal OM, respectively (Figure 11). The N entering the duodenum is composed of BactN, EN, and ruminally undegraded feed N (RUN), which are digested to different extents in the small intestine. The true digestibility of BactN has been estimated to be 0.82 (Storm et al., 1983a,b), and a value of 0.80 has been used for the true protein in EN (NRC, 2001), although lower values have been reported (0.6, Sandek et al., 2001). Although most of the EN enters the proximal small intestine (foregut EN, pancreatic and hepatic secretions) and thus has ample opportunity to be digested and absorbed, EN entering the distal small intestine is unlikely to be digested and its AA reabsorbed before reaching the hindgut. The third nitrogenous component of the duodenal digesta, RUN, has a variable small intestinal digestibility depending on the feedstuffs that composed the diet. Although a fixed value of 0.8 has been used for RUN in the past (NRC, 1985, 1989), a variable digestibility

between 0.5 and 1 depending on feedstuff has now been adopted (NRC, 2001).

The hindgut, like the rumen, harbors an active microbial population capable of utilizing available N. The N balance across the hindgut was negative when the ileal N content was below 31.9 g/kg of ileal OM. The true large intestinal N digestibility was 0.49, reflecting the low digestibility of the N reaching the terminal ileum.

The true digestibility of N and the EN entering the different segments can be integrated to describe the N transactions along the whole GI tract. The N transactions for the reference diet, with a N content of 24.2 g/kg of OM, are shown in Figure 14. Details of the calculations are shown in the Appendix.

Rumen available N originated from the feed (16.37 g/kg of OMI) and from EN entering the rumen (10.54 g/kg of OMI). Ruminal EN represented 39.2% of the total ruminal available N for microbial protein synthesis, a value higher than that (16%) reported by Kluth et al. (2000), but still lower than the 60% reported by Siddons et al. (1985). The diet provided 25.17 g of N/kg of OMI and 0.55 kg of OM/kg of OMI at the duodenum, and the N consisted of 56% BactN (14.05 g of N/kg of OMI), 31% RUN (7.83 g of N/kg of OMI), and 13% free EN (3.29 g of N/kg of OMI). The proportion of free EN in duodenal contents shows good agreement with values reported in the literature (9 to 12%, Brandt et al., 1980; 8%, Van Bruchem et al., 1997; 12%, Ouellet et al., 2002). If rumen microbes do not discriminate between feed N and EN for microbial protein synthesis, 5.50 g of BactN/kg of OMI originated from EN. Although the present approach does not allow for a differentiation between the contribution of urea N and other sources of EN, it seems that they contribute roughly equally to BactN (Ouellet et al., 2002). The duodenal entry of free EN and microbial N that originated from EN was 8.79 g of N/kg of OMI or 34.9% of the total N entering the duodenum. This last value is similar to the 31 to 37% observed by Ouellet et al. (2002) when plasma was considered as the precursor for EN. Furthermore, approximately one-third of the total duodenal N originating from endogenous sources was free EN, which agrees with the findings of these researchers.

From the duodenal inflow of N and the minimal estimate of EN (3.10 g of N/kg of OMI) that entered the small intestine, at least 18.99 g of N/kg of OMI were absorbed resulting in 9.29 g of N/kg of OMI reaching the terminal ileum. In the hindgut, an additional (minimal) 5.00 g of N/kg of OMI entered as EN, and (at least) 4.54 g of N/kg of OMI was absorbed (Figure 14). The fecal excretion resulted in 9.75 g of N/kg of OMI. For the same diet, the fecal N excretion calculated directly from the regression in Figure 2 yielded 8.13 g of N/kg of OMI.

The agreement between both methods for calculating fecal N excretion for the reference diet improved as the N content of diet increased. When the diet reached 40 g of N/kg of OM, the predictions were 10.74 and 10.62 N/kg of OMI for the indirect and direct methods, respectively. The direct method, however, was based on the

complete database, whereas the step-by-step integrative approach was based on a smaller subset. Studies with ileally cannulated cattle were less frequent (26 of 108) and ileal NDF was determined in only 8 cases.

Other limitations of the database compiled are evident. Because a meta-analysis is a summation of trials, it is only as good as the trials that are combined in the meta-analysis. As previously discussed, the drying of feces was likely to introduce a systematic bias to the values obtained. Limited descriptions of the experimental diets in some of the studies prevented a better characterization of the covariates tested. The different analytical methodologies also increased the heterogeneity of the data. The problem of heterogeneity in meta-analysis can be estimated, but confidence intervals for predicted values are larger (Burnham and Anderson, 1998). The heterogeneity of animals and diets, however, may actually strengthen the meta-analysis by allowing a generalization of the results obtained to be applied to a broader group of different conditions (Flather et al., 1997).

Some limitations were associated with the way data were reported. Some studies resorted to factorial arrangements of treatments, reporting main effects instead of the means of the actual treatments. Further, the recalculation of data prevented the estimation of the error associated with the means, and thus precluded the use of proper weighting of the means during the analysis. A relatively recent development in meta-analysis has been the pooling of individual data from the original trials (Flather et al., 1997). The advent of electronic publishing, which has largely overcome space limitations in hard-copy publishing, allows supplemental materials to be copublished, including raw data. This will allow for improvement in future analyses (Lin et al., 2004).

In summary, N is not only absorbed from the GI tract, but large quantities of N are also secreted into its lumen. This EN can account for a relatively large proportion of the N available in the rumen for microbial protein synthesis and of the total N reaching the duodenum. The contribution of EN has received little attention in the past and current estimates have been derived from data obtained in rather artificial conditions. More realistic values from cattle fed common diets are needed. Our estimates of N transactions along the GI tract of cattle represent mean values from experimental diets, most of which were fed under normal conditions.

LITERATURE CITED

- Ahvenjarvi, S., A. Vanhatalo, P. Huhtanen, and T. Varvikko. 2000. Determination of reticulo-rumen and whole-stomach digestion in lactating cows by omasal canal or duodenal sampling. *Br. J. Nutr.* 83:67–77.
- Aldrich, C. G., N. R. Merchen, D. R. Nelson, and J. A. Barmore. 1995. The effects of roasting temperature applied to whole soybeans on site of digestion by steers: II. Protein and amino acid digestion. *J. Anim. Sci.* 73:2131–2140.
- Aldrich, J. M., L. D. Muller, G. A. Varga, and L. C. Griel Jr. 1993. Nonstructural carbohydrate and protein effects on rumen fermentation, nutrient flow, and performance of dairy cows. *J. Dairy Sci.* 76:1091–1105.
- Arieli, A., S. Abramson, S. J. Mabjeesh, S. Zamwel, and I. Bruckental. 2001. Effect of site and source of energy supplementation on milk yield in dairy cows. *J. Dairy Sci.* 84:462–470.
- Barajas, R., and R. A. Zinn. 1998. The feeding value of dry-rolled and steam-flaked corn in finishing diets for feedlot cattle: Influence of protein supplementation. *J. Anim. Sci.* 76:1744–1752.
- Beauchemin, K. A., W. Z. Yang, D. P. Morgavi, G. R. Ghorbani, W. Kautz, and J. A. Leedle. 2003. Effects of bacterial direct-fed microbials and yeast on site and extent of digestion, blood chemistry, and subclinical ruminal acidosis in feedlot cattle. *J. Anim. Sci.* 81:1628–1640.
- Beauchemin, K. A., W. Z. Yang, and L. M. Rode. 2001. Effects of barley grain processing on the site and extent of digestion of beef feedlot finishing diets. *J. Anim. Sci.* 79:1925–1936.
- Bengochea, W. L., G. P. Lardy, M. L. Bauer, and S. A. Soto-Navarro. 2005. Effect of grain processing degree on intake, digestion, ruminal fermentation, and performance characteristics of steers fed medium-concentrate growing diets. *J. Anim. Sci.* 83:2815–2825.
- Bernard, J. K., P. T. Chandler, J. W. West, A. H. Parks, H. A. Amos, M. A. Froetschel, and D. S. Trammell. 2004. Effect of supplemental L-lysine-HCl and corn source on rumen fermentation and amino acid flow to the small intestine. *J. Dairy Sci.* 87:399–405.
- Berzaghi, P., J. H. Herbein, and C. E. Polan. 1996. Intake, site, and extent of nutrient digestion of lactating cows grazing pasture. *J. Dairy Sci.* 79:1581–1589.
- Bohnert, D. W., B. T. Larson, M. L. Bauer, A. F. Branco, K. R. McLeod, D. L. Harmon, and G. E. Mitchell Jr. 1998. Nutritional evaluation of poultry by-product meal as a protein source for ruminants: Effects on performance and nutrient flow and disappearance in steers. *J. Anim. Sci.* 76:2474–2484.
- Bohnert, D. W., C. S. Schauer, L. Bauert, and T. DelCurto. 2002. Influence of rumen protein degradability and supplementation frequency on steers consuming low-quality forage: I. Site of digestion and microbial efficiency. *J. Anim. Sci.* 80:2967–2977.
- Boss, D. L., and J. G. Bowman. 1996. Barley varieties for finishing steers: II. Ruminal characteristics and rate, site, and extent of digestion. *J. Anim. Sci.* 74:1973–1981.
- Bourquin, L. D., E. C. Titgemeyer, N. R. Merchen, and G. C. Fahey, Jr. 1994. Forage level and particle size effects on orchardgrass digestion by steers: I. Site and extent of organic matter, nitrogen, and cell wall digestion. *J. Anim. Sci.* 72:746–758.
- Brandt, M., K. Rohr, and P. Lebzien. 1980. Determination of endogenous protein-N in duodenal chyme of dairy-cows using of N-15. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 44:26–27.
- Burnham, K. P., and D. R. Anderson. 1998. Model Selection and Inference. A Practical Information-Theoretic Approach. Springer-Verlag, New York, NY.
- Callison, S. L., J. L. Firkins, M. L. Eastridge, and B. L. Hull. 2001. Site of nutrient digestion by dairy cows fed corn of different particle sizes or steam-rolled. *J. Dairy Sci.* 84:1458–1467.
- Cameron, M. R., T. H. Klusmeyer, G. L. Lynch, J. H. Clark, and D. R. Nelson. 1991. Effects of urea and starch on rumen fermentation, nutrient passage to the duodenum, and performance of cows. *J. Dairy Sci.* 74:1321–1336.
- Caton, J. S., J. E. Williams, T. May, E. E. Beaver, and R. L. Belyea. 1991. Evaluation of dairy food processing wash water solids as a protein source: I. Forage intake, animal performance, ruminal fermentation, and site of digestion in heifers fed medium-quality hay. *J. Anim. Sci.* 69:3406–3415.
- Cecava, M. J., N. R. Merchen, L. L. Berger, R. I. Mackie, and G. C. Fahey Jr. 1991. Effects of dietary energy level and protein source on nutrient digestion and ruminal nitrogen metabolism in steers. *J. Anim. Sci.* 69:2230–2243.
- Cecava, M. J., N. R. Merchen, L. L. Berger, and D. R. Nelson. 1990. Effect of energy level and feeding frequency on site of digestion and postruminal nutrient flows in steers. *J. Dairy Sci.* 73:2470–2479.

- Cecava, M. J., and J. E. Parker. 1993. Intestinal supply of amino acids in steers fed ruminally degradable and undegradable crude protein sources alone and in combination. *J. Anim. Sci.* 71:1596–1605.
- Choat, W. T., C. R. Krehbiel, M. S. Brown, G. C. Duff, D. A. Walker, and D. R. Gill. 2002. Effects of restricted versus conventional dietary adaptation on feedlot performance, carcass characteristics, site and extent of digestion, digesta kinetics, and ruminal metabolism. *J. Anim. Sci.* 80:2726–2739.
- Christiansen, M. L., and K. E. Webb, Jr. 1990. Intestinal acid flow, dry matter, starch and protein digestibility and amino acid absorption in beef cattle fed a high-concentrate diet with defluorinated rock phosphate, limestone or magnesium oxide. *J. Anim. Sci.* 68:2105–2118.
- Chung, Y. H., H. G. Bateman, II, C. C. Williams, C. C. Stanley, D. T. Gantt, T. W. Braud, L. L. Southern, J. D. Ward, P. G. Hoyt, and G. A. Sod. 2006. Effects of methionine and lysine on fermentation in vitro and in vivo, nutrient flow to the intestine, and milk production. *J. Dairy Sci.* 89:1613–1620.
- Coomer, J. C., H. E. Amos, M. A. Froetschel, K. K. Ragland, and C. C. Williams. 1993. Effects of supplemental protein source on ruminal fermentation, protein degradation, and amino acid absorption in steers and on growth and feed efficiency in steers and heifers. *J. Anim. Sci.* 71:3078–3086.
- Corona, L., F. N. Owens, and R. A. Zinn. 2006. Impact of corn vitreousness and processing on site and extent of digestion by feedlot cattle. *J. Anim. Sci.* 84:3020–3031.
- Crocker, L. M., E. J. DePeters, J. G. Fadel, H. Perez-Monti, S. J. Taylor, J. A. Wyckoff, and R. A. Zinn. 1998. Influence of processed corn grain in diets of dairy cows on digestion of nutrients and milk composition. *J. Dairy Sci.* 81:2394–2407.
- Cunningham, K. D., M. J. Cecava, and T. R. Johnson. 1994. Flows of nitrogen and amino acids in dairy cows fed diets containing supplemental feather meal and blood meal. *J. Dairy Sci.* 77:3666–3675.
- Currier, T. A., D. W. Bohnert, S. J. Falck, C. S. Schauer, and S. J. Bartle. 2004. Daily and alternate-day supplementation of urea or biuret to ruminants consuming low-quality forage: II. Effects on site of digestion and microbial efficiency in steers. *J. Anim. Sci.* 82:1518–1527.
- Doreau, M., A. Ferlay, and Y. Elmeddah. 1993. Organic matter and nitrogen digestion by dairy cows fed calcium salts of rapeseed oil fatty acids or rapeseed oil. *J. Anim. Sci.* 71:499–504.
- Egan, J. K., and P. T. Doyle. 1984. A comparison of particulate markers for the estimation of digesta flow from the abomasum of sheep offered chopped oaten hay. *Aust. J. Agric. Res.* 35:279–291.
- Elizalde, J. C., J. D. Cremin Jr., D. B. Faulkner, and N. R. Merchen. 1998. Performance and digestion by steers grazing tall fescue and supplemented with energy and protein. *J. Anim. Sci.* 76:1691–1701.
- Elizalde, J. C., N. R. Merchen, and D. B. Faulkner. 1999. Supplemental cracked corn for steers fed fresh alfalfa: II. Protein and amino acid digestion. *J. Anim. Sci.* 77:467–475.
- Erasmus, L. J., P. M. Botha, and A. Kistner. 1992. Effect of yeast culture supplement on production, rumen fermentation, and duodenal nitrogen flow in dairy cows. *J. Dairy Sci.* 75:3056–3065.
- Faichney, G. A., and G. A. White. 1988. Rates of passage of solutes, microbes and particulate matter through the gastrointestinal tract of ewes fed at a constant rate throughout gestation. *Aust. J. Agric. Res.* 39:481–492.
- Fan, M. Z., W. C. Sauer, and M. I. McBurney. 1995. Estimation by regression-analysis of endogenous amino acid levels in digesta collected from the distal ileum of pigs. *J. Anim. Sci.* 73:2319–2328.
- Flather, M. D., M. E. Farkouh, J. M. Pogue, and S. Yusuf. 1997. Strengths and limitations of meta-analysis: Larger studies may be more reliable. *Control. Clin. Trials* 18:568–579. Discussion 661–666.
- Flatt, W. P., H. F. Richter, D. R. Gillian, and H. F. Lawson. 1961. Comparative study of freezing, canning, and drying for preservation. Downloaded from jas.fass.org at USDA Natl Agricultural Library on June 3, 2008.
- Fuller, M. F., and P. J. Reeds. 1998. Nitrogen cycling in the gut. *Annu. Rev. Nutr.* 18:385–411.
- Galloway, D. L., Sr., A. L. Goetsch, L. A. Forster Jr., A. C. Brake, and Z. B. Johnson. 1993. Digestion, feed intake, and live weight gain by cattle consuming bermudagrass and supplemented with different grains. *J. Anim. Sci.* 71:1288–1297.
- Garcia, S. C., F. J. Santini, and J. C. Elizalde. 2000. Sites of digestion and bacterial protein synthesis in dairy heifers fed fresh oats with or without corn or barley grain. *J. Dairy Sci.* 83:746–755.
- Gill, M., P. H. Robinson, and J. J. Kennelly. 1999. Diurnal patterns in rumen volume and composition of digesta flowing into the duodenum. *Anim. Sci.* 69:237–249.
- Greenfield, T. L., R. L. Baldwin VI, R. A. Erdman, and K. R. McLeod. 2001. Ruminant fermentation and intestinal flow of nutrients by lactating cows consuming brown midrib corn silages. *J. Dairy Sci.* 84:2469–2477.
- Grigsby, K. N., M. S. Kerley, J. A. Paterson, and J. C. Weigel. 1992. Site and extent of nutrient digestion by steers fed a low-quality brome grass hay diet with incremental levels of soybean hull substitution. *J. Anim. Sci.* 70:1941–1949.
- Grigsby, K. N., M. S. Kerley, J. A. Paterson, and J. C. Weigel. 1993. Combinations of starch and digestible fiber in supplements for steers consuming a low-quality brome grass hay diet. *J. Anim. Sci.* 71:1057–1064.
- Gunter, S. A., L. J. Krysl, M. B. Judkins, J. T. Broesder, and R. K. Barton. 1990. Influence of branched-chain fatty acid supplementation on voluntary intake, site and extent of digestion, ruminal fermentation, digesta kinetics and microbial protein synthesis in beef heifers consuming grass hay. *J. Anim. Sci.* 68:2885–2892.
- Hannah, S. M., R. C. Cochran, E. S. Vanzant, and D. L. Harmon. 1991. Influence of protein supplementation on site and extent of digestion, forage intake, and nutrient flow characteristics in steers consuming dormant bluestem-range forage. *J. Anim. Sci.* 69:2624–2633.
- Harmon, D. L., and C. J. Richards. 1997. Considerations for gastrointestinal cannulations in ruminants. *J. Anim. Sci.* 75:2248–2255.
- Hart, F. J., and J. Leibholz. 1990. A note on the flow of endogenous protein to the omasum and abomasum of steers. *Anim. Prod.* 51:217–219.
- Hermesmeier, G. N., L. L. Berger, N. R. Merchen, and T. G. Nash. 2002. Effects of restricted and ad libitum intake of diets containing wheat middlings on site and extent of digestion in steers. *J. Anim. Sci.* 80:812–817.
- Herrera-Saldana, R., R. Gomez-Alarcon, M. Torabi, and J. T. Huber. 1990. Influence of synchronizing protein and starch degradation in the rumen on nutrient utilization and microbial protein synthesis. *J. Dairy Sci.* 73:142–148.
- Holter, J. A., and J. T. Reid. 1959. Relationship between the concentration of crude protein and apparently digestible protein in forages. *J. Anim. Sci.* 18:1339–1349.
- Hutchinson, J. C., and S. Morris. 1936. The digestibility of dietary protein in the ruminant: The digestibility of protein following a prolonged fast, with a detailed study of the nitrogen metabolism. *Biochem. J.* 30:1695–1704.
- Ipharraguerre, I. R., and J. H. Clark. 2005. Varying protein and starch in the diet of dairy cows. II. Effects on performance and nitrogen utilization for milk production. *J. Dairy Sci.* 88:2556–2570.
- Ipharraguerre, I. R., J. H. Clark, and D. E. Freeman. 2005. Rumen fermentation and intestinal supply of nutrients in dairy cows fed rumen-protected soy products. *J. Dairy Sci.* 88:2879–2892.
- Ipharraguerre, I. R., Z. Shabi, J. H. Clark, and D. E. Freeman. 2002. Ruminant fermentation and nutrient digestion by dairy cows fed varying amounts of soyhulls as a replacement for corn grain. *J. Dairy Sci.* 85:2890–2904.
- Jonker, J. S., R. A. Kohn, and R. A. Erdman. 1998. Using milk urea nitrogen to predict nitrogen excretion and utilization efficiency in lactating dairy cows. *J. Dairy Sci.* 81:2681–2692.

- Joy, M. T., E. J. DePeters, J. G. Fadel, and R. A. Zinn. 1997. Effects of corn processing on the site and extent of digestion in lactating cows. *J. Dairy Sci.* 80:2087–2097.
- Juko, C. D., R. M. Bredon, and B. Marshall. 1961. The nutrition of zebu cattle: Part II. The techniques of digestibility trials with special reference to sampling, preservation and drying of feces. *J. Agric. Sci.* 56:93–97.
- Kauffman, A. J., and N. R. St-Pierre. 2001. The relationship of milk urea nitrogen to urine nitrogen excretion in Holstein and Jersey cows. *J. Dairy Sci.* 84:2284–2294.
- Keery, C. M., H. E. Amos, and M. A. Froetschel. 1993. Effects of supplemental protein source on intraruminal fermentation, protein degradation, and amino acid absorption. *J. Dairy Sci.* 76:514–524.
- Khorasani, G. R., E. K. Okine, and J. J. Kennelly. 1996. Forage source alters nutrient supply to the intestine without influencing milk yield. *J. Dairy Sci.* 79:862–872.
- Khorasani, G. R., E. K. Okine, and J. J. Kennelly. 2001. Effects of forage source and amount of concentrate on rumen and intestinal digestion of nutrients in late-lactation cows. *J. Dairy Sci.* 84:1156–1165.
- Khorasani, G. R., W. C. Sauer, L. Ozimek, and J. J. Kennelly. 1990. Digestion of soybean meal and canola meal protein and amino acids in the digestive tract of young ruminants. *J. Anim. Sci.* 68:3421–3428.
- King, K. J., J. T. Huber, M. Sadik, W. G. Bergen, A. L. Grant, and V. L. King. 1990. Influence of dietary protein sources on the amino acid profiles available for digestion and metabolism in lactating cows. *J. Dairy Sci.* 73:3208–3216.
- Klusmeyer, T. H., R. D. McCarthy Jr., J. H. Clark, and D. R. Nelson. 1990. Effects of source and amount of protein on ruminal fermentation and passage of nutrients to the small intestine of lactating cows. *J. Dairy Sci.* 73:3526–3537.
- Kluth, H., M. Gabel, J. Voigt, and U. Schonhuse. 2000. The use of endogenous nitrogen for microbial crude protein synthesis in the rumen of growing bulls. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 84:136–147.
- Knowlton, K. F., B. P. Glenn, and R. A. Erdman. 1998. Performance, ruminal fermentation, and site of starch digestion in early lactation cows fed corn grain harvested and processed differently. *J. Dairy Sci.* 81:1972–1984.
- Koenig, K. M., K. A. Beauchemin, and L. M. Rode. 2003. Effect of grain processing and silage on microbial protein synthesis and nutrient digestibility in beef cattle fed barley-based diets. *J. Anim. Sci.* 81:1057–1067.
- Kohn, R. A., M. M. Dinneen, and E. Russek-Cohen. 2005. Using blood urea nitrogen to predict nitrogen excretion and efficiency of nitrogen utilization in cattle, sheep, goats, horses, pigs, and rats. *J. Anim. Sci.* 83:879–889.
- Krysl, L. J., M. B. Judkins, and V. R. Bohman. 1991. Influence of ruminal or duodenal soybean oil infusion on intake, ruminal fermentation, site and extent of digestion, and microbial protein synthesis in beef heifers consuming grass hay. *J. Anim. Sci.* 69:2585–2590.
- Lapierre, H., D. Pacheco, R. Berthiaume, D. R. Ouellet, C. G. Schwab, P. Dubreuil, G. Holtrop, and G. E. Lobley. 2006. What is the true supply of amino acids for a dairy cow? *J. Dairy Sci.* 89:E1–E14.
- Lardy, G. P., G. E. Catlett, M. S. Kerley, and J. A. Paterson. 1993. Determination of the ruminal escape value and duodenal amino acid flow of rapeseed meal. *J. Anim. Sci.* 71:3096–3104.
- Leupp, J. L., J. S. Caton, S. A. Soto-Navarro, and G. P. Lardy. 2005. Effects of cooked molasses blocks and fermentation extract or brown seaweed meal inclusion on intake, digestion, and microbial efficiency in steers fed low-quality hay. *J. Anim. Sci.* 83:2938–2945.
- Lin, Y., S. R. Dueker, J. R. Follett, J. G. Fadel, A. Arjomand, P. D. Schneider, J. W. Miller, R. Green, B. A. Buchholz, J. S. Vogel, R. D. Phair, and A. J. Clifford. 2004. Quantitation of in vivo human folate metabolism. *Am. J. Clin. Nutr.* 80:680–691.
- Ludden, P. A., and M. J. Cecava. 1995. Supplemental protein sources for steers fed corn-based diets: I. Ruminal characteristics and intestinal amino acid flows. *J. Anim. Sci.* 73:1466–1475.
- Mabjeesh, S. J., A. Arieli, I. Bruckental, S. Zamwell, and H. Tagari. 1996. Effect of type of protein supplementation on duodenal amino acid flow and absorption in lactating dairy cows. *J. Dairy Sci.* 79:1792–1801.
- Macrae, J. C., A. Walker, D. Brown, and G. E. Lobley. 1993. Accretion of total protein and individual amino acids by organs and tissues of growing lambs and the ability of nitrogen-balance techniques to quantitate protein retention. *Anim. Prod.* 57:237–245.
- May, T., J. E. Williams, and J. S. Caton. 1991. Evaluation of dairy food processing wash water solids as a protein source: III. Nitrogen utilization by heifers fed medium-concentrate diets. *J. Anim. Sci.* 69:3425–3434.
- Milton, C. T., R. T. Brandt Jr., and E. C. Titgemeyer. 1997a. Effects of dietary nitrogen source and concentration in high-grain diets on finishing steer performance and nutrient digestion. *J. Anim. Sci.* 75:2813–2823.
- Milton, C. T., R. T. Brandt Jr., and E. C. Titgemeyer. 1997b. Urea in dry-rolled corn diets: Finishing steer performance, nutrient digestion, and microbial protein production. *J. Anim. Sci.* 75:1415–1424.
- Moorby, J. M., R. J. Dewhurst, R. T. Evans, and J. L. Danelon. 2006. Effects of dairy cow diet forage proportion on duodenal nutrient supply and urinary purine derivative excretion. *J. Dairy Sci.* 89:3552–3562.
- Murphy, T. A., S. C. Loerch, and B. A. Dehority. 1994. The influence of restricted feeding on site and extent of digestion and flow of nitrogenous compounds to the duodenum in steers. *J. Anim. Sci.* 72:2487–2496.
- NRC. 1985. Ruminant Nitrogen Usage. Natl. Acad. Press, Washington, DC.
- NRC. 1989. Nutrient Requirements of Dairy Cattle. 6th rev. ed. Update. Natl. Acad. Press, Washington, DC.
- NRC. 2001. Nutrient Requirements of Dairy Cattle. 7th rev. ed. Natl. Acad. Press, Washington, DC.
- Oba, M., and M. S. Allen. 2003. Effects of diet fermentability on efficiency of microbial nitrogen production in lactating dairy cows. *J. Dairy Sci.* 86:195–207.
- Obispo, N. E., and B. A. Dehority. 1999. Feasibility of using total purines as a marker for ruminal bacteria. *J. Anim. Sci.* 77:3084–3095.
- Oliveira, J. S., J. T. Huber, J. M. Simas, C. B. Theurer, and R. S. Swingle. 1995. Effect of sorghum grain processing on site and extent of digestion of starch in lactating dairy cows. *J. Dairy Sci.* 78:1318–1327.
- Olson, K. C., J. S. Caton, D. R. Kirby, and P. L. Norton. 1994. Influence of yeast culture supplementation and advancing season on steers grazing mixed-grass prairie in the northern Great Plains: II. Ruminal fermentation, site of digestion, and microbial efficiency. *J. Anim. Sci.* 72:2158–2170.
- Orskov, E. R., N. A. MacLeod, and D. J. Kyle. 1986. Flow of nitrogen from the rumen and abomasum in cattle and sheep given protein-free nutrients by intragastric infusion. *Br. J. Nutr.* 56:241–248.
- Ouellet, D. R., M. Demers, G. Zuur, G. E. Lobley, J. R. Seoane, J. V. Nolan, and H. Lapierre. 2002. Effect of dietary fiber on endogenous nitrogen flows in lactating dairy cows. *J. Dairy Sci.* 85:3013–3025.
- Overton, T. R., M. R. Cameron, J. P. Elliott, J. H. Clark, and D. R. Nelson. 1995. Ruminal fermentation and passage of nutrients to the duodenum of lactating cows fed mixtures of corn and barley. *J. Dairy Sci.* 78:1981–1998.
- Palmquist, D. L., M. R. Weisbjerg, and T. Hvelplund. 1993. Ruminal, intestinal, and total digestibilities of nutrients in cows fed diets high in fat and undegradable protein. *J. Dairy Sci.* 76:1353–1364.
- Perez, J. F., J. Balcells, J. A. Guada, and C. Castrillo. 1996. Determination of rumen microbial-nitrogen production in sheep: A comparison of urinary purine excretion with methods using of N-15 and purine bases as markers of microbial-nitrogen entering the duodenum. *Br. J. Nutr.* 75:699–709.
- Philippeau, C., C. Martin, and B. Michalet-Doreau. 1999. Influence of grain source on ruminal characteristics and rate, site, and extent of digestion in beef steers. *J. Anim. Sci.* 77:1587–1596.

- Poore, M. H., J. A. Moore, T. P. Eck, R. S. Swingle, and C. B. Theurer. 1993. Effect of fiber source and ruminal starch degradability on site and extent of digestion in dairy cows. *J. Dairy Sci.* 76:2244–2253.
- Punia, B. S., J. Leibholz, and G. J. Faichney. 1989. Effects of level of intake and urea supplementation of alkali-treated straw on protozoal and bacterial nitrogen synthesis in the rumen and partition of digestion in cattle. *Aust. J. Agric. Res.* 39:1181–1194.
- Qiu, X., M. L. Eastridge, and J. L. Firkins. 2004. Effects of dry matter intake, addition of buffer, and source of fat on duodenal flow and concentration of conjugated linoleic acid and *trans*-11 C18:1 in milk. *J. Dairy Sci.* 87:4278–4286.
- Rasch, T. W., and N. J. Benevenga. 2004. Recovery of N-15 in the body, urine, and gas phase of piglets infused intravenously with N-15 L-alanine from 12–72 hours of age. *J. Nutr.* 134:847–854.
- Reed, J. J., A. L. Gelvin, G. P. Lardy, M. L. Bauer, and J. S. Caton. 2006. Effect of creep feed supplementation and season on intake, microbial protein synthesis and efficiency, ruminal fermentation, digestion, and performance in nursing calves grazing native range in southeastern North Dakota. *J. Anim. Sci.* 84:411–423.
- Remond, D., J. I. Cabrera-Estrada, M. Champion, B. Chauveau, R. Coudure, and C. Poncet. 2004. Effect of corn particle size on site and extent of starch digestion in lactating dairy cows. *J. Dairy Sci.* 87:1389–1399.
- Robinson, P. H., G. Coto, M. D. Stern, and D. M. Veira. 1990. Interlaboratory variation in a diaminopimelic acid assay: Influence on estimated duodenal bacterial nitrogen flow. *J. Dairy Sci.* 73:2929–2933.
- Robinson, P. H., and J. J. Kennelly. 1990. Evaluation of a duodenal cannula for dairy cattle. *J. Dairy Sci.* 73:3146–3157.
- Robinson, P. H., G. R. Khorasani, and J. J. Kennelly. 1994. Forestomach and whole tract digestion in lactating dairy cows fed canola meal treated with variable levels of acetic acid. *J. Dairy Sci.* 77:552–559.
- Sadik, M. S., J. T. Huber, K. King, R. Wanderley, D. DeYoung, A. al-Dehneh, and C. Dudas. 1990. Comparison of nitrogen-15 and diaminopimelic acid for estimating bacterial protein synthesis of lactating cows fed diets of varying protein degradability. *J. Dairy Sci.* 73:694–702.
- Sairanen, A., H. Khalili, J. I. Nousiainen, S. Ahvenjarvi, and P. Huttanen. 2005. The effect of concentrate supplementation on nutrient flow to the omasum in dairy cows receiving freshly cut grass. *J. Dairy Sci.* 88:1443–1453.
- Sandek, A., K. Krawielitzki, J. Kowalczyk, F. Kreienbring, U. Schonhusen, M. Gabel, T. Zebrowska, H. Hagemeister, and J. Voigt. 2001. Studies on N-metabolism in different gastro-intestinal sections of sheep using the digesta exchange technique. 2. Passage of endogenous nitrogen. *J. Anim. Feed Sci.* 10:605–618.
- Scholljegerdes, E. J., B. W. Hess, G. E. Moss, D. L. Hixon, and D. C. Rule. 2004a. Influence of supplemental cracked high-linoleate or high-oleate safflower seeds on site and extent of digestion in beef cattle. *J. Anim. Sci.* 82:3577–3588.
- Scholljegerdes, E. J., P. A. Ludden, and B. W. Hess. 2004b. Site and extent of digestion and amino acid flow to the small intestine in beef cattle consuming limited amounts of forage. *J. Anim. Sci.* 82:1146–1156.
- Scholljegerdes, E. J., T. R. Weston, P. A. Ludden, and B. W. Hess. 2005. Supplementing a ruminally undegradable protein supplement to maintain essential amino acid supply to the small intestine when forage intake is restricted in beef cattle. *J. Anim. Sci.* 83:2151–2161.
- Siddons, R. C., D. E. Beever, and J. V. Nolan. 1982. A comparison of methods for the estimation of microbial nitrogen in duodenal digesta of sheep. *Br. J. Nutr.* 48:377–389.
- Siddons, R. C., J. V. Nolan, D. E. Beever, and J. C. Macrae. 1985. Nitrogen digestion and metabolism in sheep consuming diets containing contrasting forms and levels of N. *Br. J. Nutr.* 54:175–187.
- Sindt, J. J., J. S. Drouillard, E. C. Titgemeyer, S. P. Montgomery, E. R. Loe, B. E. Depenbusch, and P. H. Walz. 2006. Influence of steam-flaked corn moisture level and density on the site and extent of digestibility and feeding value for finishing cattle. *J. Anim. Sci.* 84:424–432.
- Sniffen, C. J., J. D. O'Connor, P. J. Van Soest, D. G. Fox, and J. B. Russell. 1992. A net carbohydrate and protein system for evaluating cattle diets. 2. Carbohydrate and protein availability. *J. Anim. Sci.* 70:3562–3577.
- Soto-Navarro, S. A., M. H. Knight, G. P. Lardy, M. L. Bauer, and J. S. Caton. 2004. Effect of fiber-based creep feed on intake, digestion, ruminal fermentation, and microbial efficiency in nursing calves. *J. Anim. Sci.* 82:3560–3566.
- Spanghero, M., and Z. M. Kowalski. 1997. Critical analysis of N balance experiments with lactating cows. *Livest. Prod. Sci.* 52:113–122.
- Stern, M. D., G. A. Varga, J. H. Clark, J. L. Firkins, J. T. Huber, and D. L. Palmquist. 1994. Evaluation of chemical and physical properties of feeds that affect protein metabolism in the rumen. *J. Dairy Sci.* 77:2762–2786.
- Storm, E., D. S. Brown, and E. R. Orskov. 1983a. The nutritive value of rumen micro-organisms in ruminants. 3. The digestion of microbial amino and nucleic acids in, and losses of endogenous nitrogen from, the small intestine of sheep. *Br. J. Nutr.* 50:479–485.
- Storm, E., E. R. Orskov, and R. Smart. 1983b. The nutritive value of rumen micro-organisms in ruminants. 2. The apparent digestibility and net utilization of microbial N for growing lambs. *Br. J. Nutr.* 50:471–478.
- St-Pierre, N. R. 2001. Invited review: Integrating quantitative findings from multiple studies using mixed model methodology. *J. Dairy Sci.* 84:741–755.
- Streeter, M. N., D. G. Wagner, C. A. Hibberd, and F. N. Owens. 1990a. Comparison of corn with 4 sorghum grain hybrids—Site and extent of digestion in steers. *J. Anim. Sci.* 68:3429–3440.
- Streeter, M. N., D. G. Wagner, C. A. Hibberd, and F. N. Owens. 1990b. The effect of sorghum grain variety on site and extent of digestion in beef heifers. *J. Anim. Sci.* 68:1121–1132.
- Sultan, J. I., F. L. Fluharty, J. L. Firkins, and S. C. Loerch. 1992. Effects of supplemental protein source and alkaline hydrogen peroxide treatment of wheat straw on site of nutrient digestion and flow of nitrogenous compounds to the duodenum of steers. *J. Anim. Sci.* 70:3909–3915.
- Swanson, E. W. 1977. Factors for computing requirements of protein for maintenance of cattle. *J. Dairy Sci.* 60:1583–1593.
- Swingle, R. S., T. P. Eck, C. B. Theurer, M. De la Llata, M. H. Poore, and J. A. Moore. 1999. Flake density of steam-processed sorghum grain alters performance and sites of digestibility by growing-finishing steers. *J. Anim. Sci.* 77:1055–1065.
- Taylor, C. C., and M. S. Allen. 2005. Corn grain endosperm type and brown midrib 3 corn silage: Ruminal fermentation and N partitioning in lactating cows. *J. Dairy Sci.* 88:1434–1442.
- Teller, E., M. Vanbelle, M. Foulon, G. Collignon, and B. Matatu. 1992. Nitrogen metabolism in rumen and whole digestive tract of lactating dairy cows fed grass silage. *J. Dairy Sci.* 75:1296–1304.
- Theurer, C. B., O. Lozano, A. Alio, A. Delgado-Elorduy, M. Sadik, J. T. Huber, and R. A. Zinn. 1999. Steam-processed corn and sorghum grain flaked at different densities alter ruminal, small intestinal, and total tract digestibility of starch by steers. *J. Anim. Sci.* 77:2824–2831.
- Tice, E. M., M. L. Eastridge, and J. L. Firkins. 1993. Raw soybeans and roasted soybeans of different particle sizes. 1. Digestibility and utilization by lactating cows. *J. Dairy Sci.* 76:224–235.
- Valkeners, D., A. Thewis, F. Piron, and Y. Beckers. 2004. Effect of imbalance between energy and nitrogen supplies on microbial protein synthesis and nitrogen metabolism in growing double-musled Belgian Blue bulls. *J. Anim. Sci.* 82:1818–1825.
- Van Bruchem, J., L. Bongers, S. C. W. Lammerswienhoven, G. A. Bangma, and P. W. M. Vanadrichem. 1989. Apparent and true digestibility of protein and amino-acids in the small-intestine of sheep as related to the duodenal passage of protein and non-protein dry-matter. *Livest. Prod. Sci.* 23:317–327.
- Van Bruchem, J., J. Voigt, T. Lammers Wienhoven, U. Schonhusen, J. Ketelaars, and S. Tamminga. 1997. Secretion and reabsorption of nitrogen in the small intestine of sheep. *J. Anim. Sci.* 84:741–755.

- tion of endogenous protein along the small intestine of sheep: Estimates derived from N-15 dilution of plasma non-protein-N. *Br. J. Nutr.* 77:273–286.
- Van Soest, P. J. 1994. *Nutritional Ecology of the Ruminant*. 2nd ed. Cornell University Press, Ithaca, NY.
- Van Vuuren, A. M., F. Krol-Kramer, R. A. van der Lee, and H. Corbijn. 1992. Protein digestion and intestinal amino acids in dairy cows fed fresh *Lolium perenne* with different nitrogen contents. *J. Dairy Sci.* 75:2215–2225.
- Van Vuuren, A. M., C. J. Van der Koelen, and J. Vroons-De Bruin. 1993. Ryegrass versus corn starch or beet pulp fiber diet effects on digestion and intestinal amino acids in dairy cows. *J. Dairy Sci.* 76:2692–2700.
- Voelker, J. A., and M. S. Allen. 2003. Pelleted beet pulp substituted for high-moisture corn: 3. Effects on ruminal fermentation, pH, and microbial protein efficiency in lactating dairy cows. *J. Dairy Sci.* 86:3562–3570.
- Waldo, D. R., and B. P. Glenn. 1984. Comparison of new protein systems for lactating dairy-cows. *J. Dairy Sci.* 67:1115–1133.
- Whitelaw, F. G., J. M. Eadie, L. A. Bruce, and W. J. Shand. 1984. Microbial protein synthesis in cattle given roughage-concentrate and all-concentrate diets: The use of 2,6-diaminopimelic acid, 2-aminoethylphosphonic acid and 35S as markers. *Br. J. Nutr.* 52:249–260.
- Yang, W. Z., and K. A. Beauchemin. 2004. Grain processing, forage-to-concentrate ratio, and forage length effects on ruminal nitrogen degradation and flows of amino acids to the duodenum. *J. Dairy Sci.* 87:2578–2590.
- Yang, W. Z., K. A. Beauchemin, K. M. Koenig, and L. M. Rode. 1997. Comparison of hull-less barley, barley, or corn for lactating cows: Effects on extent of digestion and milk production. *J. Dairy Sci.* 80:2475–2486.
- Zinn, R. A. 1990. Influence of steaming time on site of digestion of flaked corn in steers. *J. Anim. Sci.* 68:776–781.
- Zinn, R. A. 1993a. Characteristics of ruminal and total tract digestion of canola meal and soybean meal in a high-energy diet for feedlot cattle. *J. Anim. Sci.* 71:796–801.
- Zinn, R. A. 1993b. Influence of oral antibiotics on digestive function in Holstein steers fed a 71% concentrate diet. *J. Anim. Sci.* 71:213–217.
- Zinn, R. A. 1993c. Influence of processing on the comparative feeding value of barley for feedlot cattle. *J. Anim. Sci.* 71:3–10.
- Zinn, R. A. 1993d. Influence of processing on the feeding value of oats for feedlot cattle. *J. Anim. Sci.* 71:2303–2309.
- Zinn, R. A. 1994. Influence of flake thickness on the feeding value of steam-rolled wheat for feedlot cattle. *J. Anim. Sci.* 72:21–28.
- Zinn, R. A., E. G. Alvarez, M. F. Montano, A. Plascencia, and J. E. Ramirez. 1998. Influence of tempering on the feeding value of rolled corn in finishing diets for feedlot cattle. *J. Anim. Sci.* 76:2239–2246.
- Zinn, R. A., and R. Barajas. 1997. Comparative ruminal and total tract digestion of a finishing diet containing fresh vs air-dry steam-flaked corn. *J. Anim. Sci.* 75:1704–1707.
- Zinn, R. A., and R. Barajas. 1997. Influence of flake density on the comparative feeding value of a barley-corn blend for feedlot cattle. *J. Anim. Sci.* 75:904–909.
- Zinn, R. A., R. Barajas, M. Montano, and R. A. Ware. 2003. Influence of dietary urea level on digestive function and growth performance of cattle fed steam-flaked barley-based finishing diets. *J. Anim. Sci.* 81:2383–2389.
- Zinn, R. A., and J. L. Borques. 1993. Influence of sodium bicarbonate and monensin on utilization of a fat-supplemented, high-energy growing-finishing diet by feedlot steers. *J. Anim. Sci.* 71:18–25.
- Zinn, R. A., and F. N. Owens. 1986. A rapid procedure for purine measurement and its use for estimating net ruminal protein-synthesis. *Can. J. Anim. Sci.* 66:157–166.
- Zinn, R. A., and F. N. Owens. 1993. Ruminal escape protein for lightweight feedlot calves. *J. Anim. Sci.* 71:1677–1687.
- Zinn, R. A., and A. Plascencia. 1993. Interaction of whole cottonseed and supplemental fat on digestive function in cattle. *J. Anim. Sci.* 71:11–17.

APPENDIX

The following calculations describe the N transactions for the reference diet (Figure 14) along the whole GI tract of cattle and are based on the intercepts and slopes shown in Figures 2, 5, 7, 9, 11, and 13. The reference diet OM basis, contained 32% NDF and carbohydrates of medium fermentation rate, ingested at an intake level of 2% of BW daily. For this simulation, a dietary N content of 24.2 g/kg of OM intake (**OMI**) was utilized. Digesta passage to the duodenum and hindgut for this diet was 0.55 and 0.32 kg of OM/kg of OMI (see below), respectively.

Rumen available N (**RDN**) originating from feed was calculated by multiplying the N content of the diet (dietary N) by the ruminal degradability of feed N (N_{degrad} , Figure 7), as

$$\text{RDN} = \text{dietary N} \times N_{\text{degrad}}, \text{ and} \quad [1]$$

$$\text{RDn} = 24.2 \text{ g/kg of OMI} \times 0.676 = 16.37 \text{ g/kg of OMI},$$

and the minimal amount of endogenous N (**EN**) entering the rumen and used for microbial synthetic processes was computed from the intercept shown in Appendix Figure 9 (10.54 g/kg of OMI). [2]

Thus the minimal contribution of ruminal EN (**ENR**) to the total N available in the rumen was

$$\text{ENR} (\%) = 10.54 / (10.54 + 16.37) = 39.2\%. \quad [3]$$

Microbial N (**BactN**) was calculated utilizing the coefficients shown in Figure 9, as

$$\begin{aligned} \text{Bactn} &= 0.145 \times 24.2 \text{ g/kg of OMI} \\ &+ 10.54 \text{ g/kg of OMI} = 14.05 \text{ g/kg of OMI}, \end{aligned} \quad [4]$$

and the minimal contribution of ruminal EN to BactN was calculated assuming that N degraded in the foregut behaved similarly, independently of its origin, as follows:

$$\begin{aligned} \text{ENR} \rightarrow \text{Bactn} &= 39.2\% \times \\ 14.05 \text{ g/kg of OMI} &= 5.50 \text{ g/kg of OMI}. \end{aligned} \quad [5]$$

Total duodenal N (**DN**), the total N exiting the foregut and entering the duodenum, was calculated based on N intake and ruminal N balance (RAD, Figure 5), as

$$\begin{aligned} \text{DN} &= \text{NI} - \text{RAD}, \text{ and } \text{DN} = 24.2 \text{ g/kg of OMI} - \\ &(0.512 \times 24.2 \text{ g/kg of OMI} - \\ 13.36 \text{ g/kg of OMI}) &= 25.17 \text{ g/kg of OMI}. \end{aligned} \quad [6]$$

The N absorbed by the foregut was then calculated by mass difference between inputs (dietary N and ENR) and output (N passage to the duodenum), as follows:

$$\begin{aligned} \text{N absorbed} &= \text{dietary N} + \text{ENR} \\ - \text{DN, and N absorbed} &= 24.2 + 10.54 \quad [7] \\ - 25.17 &= 9.57 \text{ g/kg of OMI.} \end{aligned}$$

The ruminal undegraded feed N (**RUN**) was estimated by difference between N intake and feed N degraded in the rumen, as

$$\text{RUN} = 24.2 - 16.37 = 7.83 \text{ g/kg of OMI.} \quad [8]$$

The free EN reaching the duodenum (**END**) was obtained by the difference between total N entering the duodenum and the contributions made by BactN and RUN, as

$$\begin{aligned} \text{END} &= \text{DN} - \text{BactN} - \text{RUN, and} \quad [9] \\ \text{END} &= 25.17 - 14.05 - 7.83 = 3.29 \text{ g/kg of OMI.} \end{aligned}$$

The contribution of each source of duodenal N can then be calculated as a percentage of the total (56% for BactN, 31% RUN, and 13% free EN). The contribution of endogenous N to the duodenal N flow (**TEND**) can be either directly as free EN or as EN incorporated into BactN, and can be calculated by addition, as follows:

$$\begin{aligned} \text{TEND} &= \text{ENR} \rightarrow \text{BactN} + \text{END, and} \quad [10] \\ \text{TEND} &= 5.50 + 3.29 = 8.79 \text{ g/kg of OMI.} \end{aligned}$$

The amount of OM reaching the duodenum was estimated (0.55 g of OM/kg of OMI) based on Table 3 and the N absorbed in the small intestine (**SIDN**) was calculated utilizing the true digestibility coefficient (0.754) from Figure 11, as

$$\begin{aligned} \text{SIDN} &= 25.17 \text{ g/kg of OMI} \quad [11] \\ \times 0.754 &= 18.99 \text{ g/kg of OMI,} \end{aligned}$$

and the minimal amount of EN entering the small intestine (**ENSI**) was estimated based on the intercept of

the SID equation and the entry of duodenal OM/OMI, as follows:

$$\begin{aligned} \text{ENSI} &= 5.60 \text{ g/kg of duodenal OM} \\ \times 0.55 \text{ kg of duodenal OM/kg of OMI} &= \quad [12] \\ 3.10 \text{ g/kg of OMI.} \end{aligned}$$

Total ileal N (**TIN**), the N reaching the terminal ileum/entering the hindgut, was calculated as

$$\begin{aligned} \text{TIN} &= \text{DN} + \text{ENSI} - \text{SIDN, and} \quad [13] \\ \text{TIN} &= 25.17 + 3.10 - 18.99 = 9.29 \text{ g/kg of OMI.} \end{aligned}$$

The amount of OM reaching the hindgut was calculated (0.32 kg of OM/kg of OMI) based on Table 3, and the EN entering the large intestine (**ENLI**) was estimated based on the entry of OM, as follows:

$$\begin{aligned} \text{ENLI} &= 15.6 \text{ g/kg of ileal OM} \quad [14] \\ \times 0.32 \text{ kg of ileal OM/kg of OMI} &= 5.00 \text{ g/kg of OMI,} \end{aligned}$$

and the N absorbed in the large intestine (**LIDN**), based on the true digestibility of N in the hindgut (Figure 13), was calculated as

$$\text{LIDN} = 9.29 \times 0.489 = 4.54 \text{ g/kg of OMI.} \quad [15]$$

The N excreted in feces can then be obtained by difference:

$$\begin{aligned} \text{FN} &= \text{TIN} + \text{ENLI} - \text{LIDN, and} \quad [16] \\ \text{FN} &= 9.29 + 5.00 - 4.54 = 9.75 \text{ g/kg of OMI.} \end{aligned}$$

Alternatively, fecal N can be calculated directly from coefficients in Figure 2, as

$$\begin{aligned} \text{FN} &= 24.2 \times (1 - 0.842) \quad [17] \\ + 4.3 &= 8.13 \text{ g/kg of OMI.} \end{aligned}$$

References

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